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

3

4 **ACCEPTED – JOURNAL OF ECOLOGY 2019**

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6 Hannah L. Mossman¹ Alastair Grant² Anthony J. Davy³

7

8 ¹ School of Science and the Environment, Manchester Metropolitan University, Manchester,
9 M1 5GD, UK

10 ² School of Environmental Sciences, University of East Anglia, Norwich Research Park,
11 Norwich, NR4 7TJ, UK

12 ³School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich,
13 NR4 7TJ, UK

14

15 Correspondence

16 Hannah L. Mossman

17 Email: h.mossman@mmu.ac.uk

18

19

20 **KEYWORDS:** coastal marsh, collinear variation, colonisation, hierarchical partitioning,
21 restoration, tidal inundation, topography, transplant, waterlogging

22

23 **Abstract**

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

54 1 INTRODUCTION

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

69 The importance of absolute elevation in the tidal frame for sediment redox potential
70 and species distributions has been well established from field measurements (Armstrong *et*
71 *al.* 1985; de la Cruz, Hackney & Bhardwaj 1989; Castillo *et al.* 2000; Anastasiou & Brooks
72 2003). However, the interpretation of causality in these relationships from field observations
73 is hampered by the strong correlations between elevation, redox potential and other variables,
74 such as salinity. At a particular tidal elevation, there is some variation in other environmental
75 conditions, which at least in part result from topographic position. For example, hummocks
76 will be less waterlogged than local depressions or pools at the same elevation. Consequently,
77 while the independent effects of these variables can be distinguished statistically (Davy *et al.*
78 2011), field experimentation is necessary to confirm causality. Some evidence derives from
79 transplanting halophytes to lower-lying sediments with a more adverse redox potential
80 (Bertness 1991; Castillo *et al.* 2000) but few studies have attempted to manipulate elevation
81 experimentally (Fragoso & Spencer 2008; Kirwan & Guntenspergen 2012; Voss, Christian &
82 Morris 2013; Kirwan & Guntenspergen 2015; Balke *et al.* 2017). Fewer of these have
83 specifically addressed redox potential (but see Ewanchuk & Bertness 2004b; Varty & Zedler
84 2008) and they generally do not attempt to distinguish the effects of absolute elevation from
85 those of local microtopography.

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

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

110

111 **2 MATERIALS AND METHODS**

112 **2.1 Study sites**

113 Experimental plots were established at three managed realignment (MR) sites in south-
114 eastern England, Brancaster in north Norfolk (52.96244° N, 0.63889° E), Freiston Shore in
115 Lincolnshire (52.96443° N, 0.09364° E) and Wallasea, Essex (51.61532° N, 0.82833° E).
116 The first two had tidal flow restored in September 2002, the last in September 2006. All were

117 relatively new MR sites and the vegetation communities on adjacent natural marshes, the
118 potential source of propagules, were similar to each other. There was no grazing by stock on
119 the areas studied and no artificial seeding or planting had been conducted prior to the
120 experiments.

121 2.2 Experimental design

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

130 Raised plots were established using sediment-retaining wooden frames (1 m x 1 m x
131 0.15 m), and transferring the top 15 cm of sediment from lowered plots, which were also
132 reinforced with wooden frames. All vegetation was removed and the sediment in the raised
133 plots allowed to settle naturally. Flat plots were established by removing all surface
134 vegetation; where this involved removing turf, sediment from nearby but outside the group of
135 plots (minimum distance of 5-10 m) was used to return the plot level to the same as the marsh
136 surface. Placement of the groups of plots was stratified across the elevation gradient of each
137 MR site, with plots haphazardly located along the gradient. Groups were a minimum of 25 m
138 apart.

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

146 In planted plots, ten plugs of each of the five species were planted in a regular grid,
147 with individuals randomly assigned to a location. Plugs were watered with locally-collected

148 seawater immediately after planting. Planting was undertaken at Brancaster and Freiston in
149 May 2010. Planting at Wallasea was delayed until early August 2010, because of concern
150 about the effects of a significant drought that occurred in May/June 2010, which coincided
151 with the period of low tides around the summer solstice. However, by October 2013 there
152 was no significant difference in survival of planted individuals between Brancaster and
153 Wallasea, but overall survival at Freiston was significantly lower than at both Brancaster and
154 Wallasea ($F_{2,493} = 97.3$, $P = 0.002$). We therefore consider there to be no effect of the timing
155 of planting, but site was also included as a term in our analyses.

156 **2.3 Field methods**

157 Surviving planted individuals were counted at the end of the growing season each year from
158 2010-2013; data presented here are from October 2013 when survival had stabilised (Fig.
159 S1). At the same time, any seedlings or established individuals of any of the five target
160 species were counted in the unplanted plots; unplanted individuals of target species that had
161 established in planted plots were also recorded. Colonisation in unplanted plots was also
162 assessed by recording the presence and percentage cover of all vascular plant species to the
163 nearest 5% (rare species were assigned a value of 1%).

164 Substrate redox potential at the centre of each experimental plot was measured in
165 June, August, September and November 2010, April, August and October 2011, and October
166 2012 and 2013, using a combination redox electrode with an Ag/AgCl reference (BDH
167 Gelplas, VWR, UK) and voltmeter (Hanna Instruments Ltd, Leighton Buzzard, UK) at 5 cm
168 depth, left until a stable reading was achieved (up to 5 minutes). Values were corrected by
169 adding the potential of the reference electrode (204 mV) with respect to a standard hydrogen
170 electrode (Eh). The mean of these nine redox values in each plot was calculated and used in
171 further analyses. The proportion of lowered plots that were full of water (i.e. ponded) was
172 recorded in June and September 2010, representing the expected lowest (June) and highest
173 (September) proportion due to the solstice and equinoctial tidal cycle. In October 2013, the
174 surface elevation relative to the UK reference level (Ordnance Datum, Newlyn (ODN)) was
175 measured at the four corners and centre of each plot (i.e. including the change in elevation
176 due to the topographic manipulation), using a differential GPS (Topcon, Newbury, UK), with
177 an accuracy of <2 cm and precision of <1.5 cm; the mean of these five measurements was
178 used as the elevation of each plot. The three sites have differing tidal regimes and so direct
179 comparison of elevation is not possible. In order to standardise elevations at the three sites to

180 their respective positions in the tidal range, and therefore allow values to be compared across
181 sites, they were expressed as tidal heights:

$$182 \quad \text{Tidal height} = (\text{Elevation relative to ODN} - \text{MHWN}) / (\text{MHWS} - \text{MHWN})$$

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

189 **2.4 Data analysis**

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

199 Total survival of all planted individuals was modelled using a generalised linear
200 model with binomial errors, with species as an explanatory variable. Significance of the
201 whole model was tested by comparing to an intercept-only null model. Survival of individual
202 species was modelled using binomial generalised linear models as a function of treatment,
203 redox potential, tidal height of the surface of the plot (i.e. including the elevation change as a
204 result of the manipulation) and site. These variables were scaled to have a mean of zero and
205 standard deviation of one to aid comparison of coefficients (mean \pm SD of each variable given
206 in Table S2). Although separate models were constructed for each species, as the scaling of
207 explanatory variables was the same in each case, model coefficients can be compared across
208 species. The independent effect of each explanatory variable was quantified using
209 hierarchical partitioning, implemented using the R package *hier.part* (Walsh & Mac Nally
210 2013). The purpose of this analysis is to identify the independent additive effects of each
211 variable. Similarly, the occurrence (presence/absence) of the most abundant species in the

212 unplanted plots was modelled as a function of treatment, redox potential, tidal height and site,
213 using generalised linear models; occurrence was selected for modelling as percentage cover
214 data were zero inflated. The six species for which there was sufficient data to model were
215 *Atriplex portulacoides*, *Puccinellia maritima*, *Salicornia europaea* agg., *Spartina anglica*,
216 *Suaeda maritima* and *Tripolium pannonicum* (*Aster tripolium*). To visualise the effect of
217 redox potential and tidal height, and explore their interaction, on plant survival in the planted
218 plots and occurrence and percentage cover (arcsine transformed) in the unplanted plots, we
219 constructed generalised additive models using the R package *mgcv* (Wood 2006), setting the
220 maximum complexity of smoothed terms to three effective degrees of freedom. We then
221 constrained predicted survival probabilities, occurrence and cover to fall within available
222 environmental space.

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

227

228 **3 RESULTS**

229 **3.1 Manipulation of microtopography significantly changed sediment oxygenation**

230 Topographic manipulation significantly altered the sediment redox potential ($F_{2,169} = 50.31$,
231 $P < 0.001$, $R^2 = 0.37$; Fig. 1a), with redox potential being significantly reduced in lowered
232 plots and increased in raised plots relative to flat plots. There was no significant difference in
233 the redox potential between planted and unplanted plots (paired Wilcoxon test: $V = 2100$, $P =$
234 0.432). Overall, redox potential was driven by elevation and treatment ($F_{5,169} = 55.59$, $P <$
235 0.001 , $R^2 = 0.62$). Elevation had a positive effect on redox potential ($\beta = 331.9 \pm 52.6$, $t =$
236 6.3 , $P < 0.001$, Fig. 1b). This relationship between tidal height and redox was not
237 significantly different between flat (control) and lowered plots ($t = 1.5$, $P = 0.144$) plots, but
238 was significantly less steep in raised plots ($t = 2.4$, $P = 0.016$). The difference in redox
239 potential between flat and lowered plots was marginally non-significant when the effect of
240 tidal height was accounted for ($t = 1.9$, $P = 0.054$), but redox remained significantly higher in
241 raised plots than in flat plots ($t = 4.0$, $P = 0.001$). Thirty percent of lowered plots were full of
242 water in June and 97% were full in September.

243 3.2 Natural vegetation establishment

244 Eleven species had colonised the unplanted plots after four years (Table S3), with *Salicornia*
245 *europaea*, *Tripolium pannonicum* and *Puccinellia maritima* occurring most frequently (72%,
246 71% and 62% of all plots respectively). Topographic manipulation influenced vegetation
247 colonisation with 49% of lowered plots remaining completely unvegetated. In contrast, little
248 bare ground remained in flat and raised plots after 4 years (Fig. 2). Natural colonisation of the
249 five species selected for planting was poor, with the exception of *Atriplex*, which occurred in
250 45% of all unplanted plots (86% of raised plots) and at high abundance (Fig. 2c, j). *Limonium*
251 colonised seven flat unplanted plots at Brancaster MR; all of these resulted from vegetative
252 growth from plants adjacent to the plot, as determined by locating vegetative runners. No
253 other planted species naturally colonised any unplanted plot. Four *Limonium* and three
254 *Plantago* seedlings established in planted plots in the immediate vicinity of planted
255 individuals that had set seed. Similarly, juvenile *Armeria* plants were found in five planted
256 plots adjacent to planted individuals; no *Triglochin* seedlings were observed.

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

270 3.3 Survival of planted individuals

271 Across all plots $35 \pm 2\%$ (mean \pm SE) of planted individuals survived to the end of the fourth
272 growing season. However, there were significant differences in survival between species
273 ($\chi^2=418.31$, $df = 4$, $P < 0.001$), with survival of *Armeria* ($13 \pm 3\%$ individuals) significantly

274 lower than that of all other species. Survival of *Atriplex* (53±5%) and *Limonium* (49±4%)
275 were significantly higher than that for *Triglochin* (33±4%) and *Plantago* (28±4%).

276 Survival of all planted species was significantly reduced in lowered plots compared to
277 both flat and raised plots (average decrease in survival ranged from 71-81%; Fig. 4, Table 2).
278 With the exception of *Triglochin*, survival of all species was significantly higher in the raised
279 plots compared to flat ones (average increase in survival, excluding *Triglochin* for which
280 there was no increase, ranged from 42-133%, Fig. 4, $P < 0.001$). This higher survival may be
281 due to the higher redox potential in raised plots, with all species having higher survival at
282 higher redox potential (Table 2) and survival of all species being poor at combinations of low
283 elevations and low redox potentials (Fig. 5). *Armeria* was confined to both the highest
284 elevations and redox potentials, not surviving at combinations of low elevation/high redox or
285 at high elevation/low redox. In contrast, survival of *Limonium* and *Triglochin* was moderate
286 (50% and 60%, respectively) in areas of high elevation/low redox. Similar to the patterns
287 seen in the occurrence and cover of naturally colonising *Atriplex* (Fig. 3), survival of planted
288 individuals was strongly influenced by redox potential (Table 2), with survival high (70%) in
289 low elevation/high redox (Fig. 5).

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

299 There were significant effects of site for all planted and unplanted species except
300 *Tripolium* (Table 1 & 2). The survival of all planted species was lower at Freiston compared
301 to Brancaster (Table 2); survival of *Atriplex* and *Plantago* were significantly higher at
302 Wallasea than Brancaster. The effects of site on the occurrence of unplanted species were
303 more variable, although occurrence tended to be higher at Brancaster than at Freiston or
304 Wallasea. The models accounted for high proportions of variance in survival or occurrence of
305 most of the species. However, models for the occurrence of *Salicornia* and *Suaeda* accounted

306 for <30% of variation, and in the planted plots variation in the survival of *Triglochin*
307 explained by the model (40%) was lower than that of the other four planted species (61-78%)
308 (Table 2).

309

310 4 DISCUSSION

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

318 By manipulating topography in the field across the whole elevation range, we had
319 plots that could be at the same elevation but had differing topography (for example, a flat plot
320 high in the marsh was at a similar elevation to a raised plot lower down the marsh (Fig. 1b)).
321 This allowed us to distinguish the effects of position in the tidal frame from those of redox
322 potential, as correlations between these variables were reduced, and to identify the
323 independent effects of topography resulting from other mechanisms. These topographic
324 manipulations altered the redox potential. Raising the local marsh level increased redox
325 potential (mean increase 100 mV), across all three sites and all elevations in the tidal range,
326 whereas local lowering of the marsh surface decreased redox potential (mean decrease of 71
327 mV); effects that were similar in magnitude to previous studies (Ewanchuk & Bertness
328 2004b; Varty & Zedler 2008). These changes in redox potential can only partly be explained
329 by alterations in the elevation (and thus inundation regime) due to raising or lowering, as
330 effects remained when elevation was accounted for, although for lowering this independent
331 effect was marginally non-significant. The increased redox potential resulting from raising
332 elevation relative to the surroundings is likely due to enhanced local drainage and hence
333 sediment oxygenation. In contrast, lowering the surface reduced the redox potential and
334 caused regular ponding in many plots. The latter suggests impeded drainage, which would
335 have lowered redox potential. The adverse redox consequences of the lowering treatment
336 were moderated somewhat at higher levels in the tidal frame, presumably because they were
337 surrounded by higher ground and, therefore, received fewer inundations than flat ground at

338 the same absolute elevation. Thus, the impact of the reduced drainage resulting from the
339 lowering could have been partially offset by having fewer inundations.

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

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

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

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

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

404 2013). Further exploration of how topography influences these would be valuable. Other
405 unmeasured biotic factors, in addition to competition, may also have influenced the
406 distribution of our species, such as differences in soil microbial communities or bioturbation
407 by benthic invertebrates (Paramor & Hughes 2005).

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

425

426 **ORCID**

427 Hannah L. Mossman <https://orcid.org/0000-0001-5958-5320>

428 Alastair Grant <https://orcid.org/0000-0002-1147-2375>

429 Anthony J. Davy <https://orcid.org/0000-0002-7658-7106>

430

431 **Data accessibility**

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

434

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441

442 **Author contributions**

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

446

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TABLES

Table 1. Coefficients (\pm 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**. $\blacksquare P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Independent effects (Ind Eff) were calculated with hierarchical partitioning.

	<i>Atriplex</i>		<i>Puccinellia</i>		<i>Salicornia</i>		<i>Spartina</i>		<i>Suaeda</i>		<i>Tripolium</i>	
	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)		-3.4 (1.26) **		-0.57 (0.45)		0.82 (0.50)		0.47 (0.35)		0.0 (0.0)	
Lowered treatment	-0.53 (0.57)	18.2	-4.54 (1.48) ***	35.0	-1.67 (0.45) ***	77.4	-11.77 (1183)†	65.5	-0.45 (0.40)	35.2	-1.35 (0.36) ***	65.4
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)		-1.44 (1.03)		-0.80 (0.36) *		-1.02 (0.49) ▪		-0.15 (0.31)		0.22 (0.40)	
Wallasea	-2.84 (1.13) *	11.0	-5.23 (1.94) *	27.8	-0.26 (0.34)	14.7	-0.85 (0.44) *	10.6	0.72 (0.33) *	23.9	-0.11 (0.37)	6.0
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 (\pm 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.

	<i>Armeria</i>		<i>Atriplex</i>		<i>Limonium</i>		<i>Plantago</i>		<i>Triglochin</i>	
	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

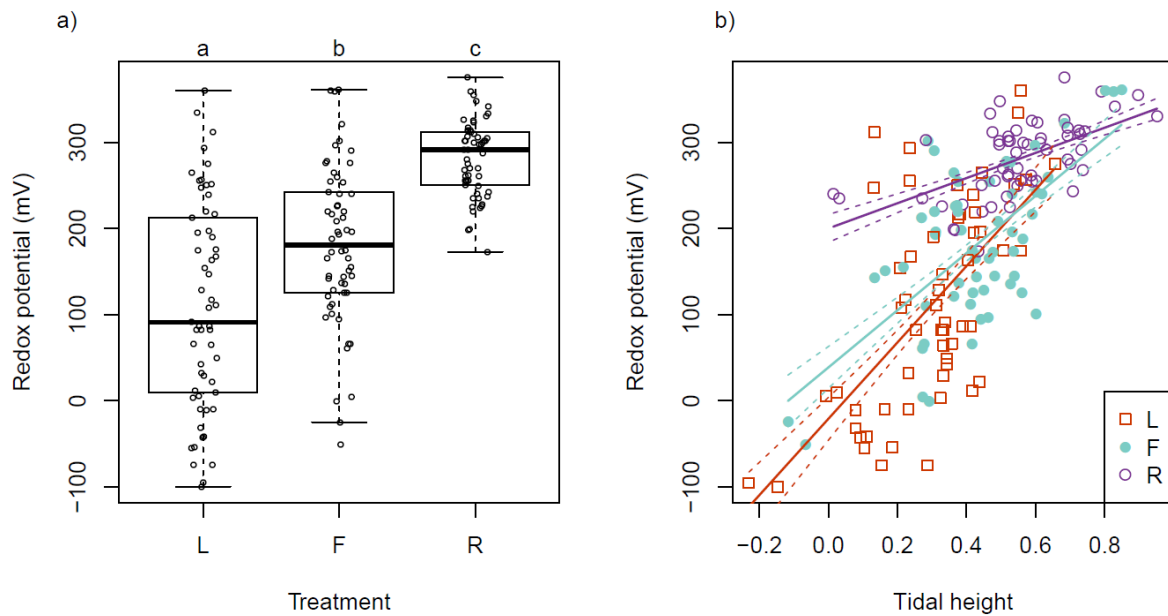


Fig. 1 (a) Sediment redox potential in planted plots with differing topographic treatments; (b) Variation in redox potential with tidal height in experimental plots. N = 172 plots. Each data point is the mean of nine values per plot taken between June 2010 and Oct 2013. L=lowered, F=flat (level with 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.

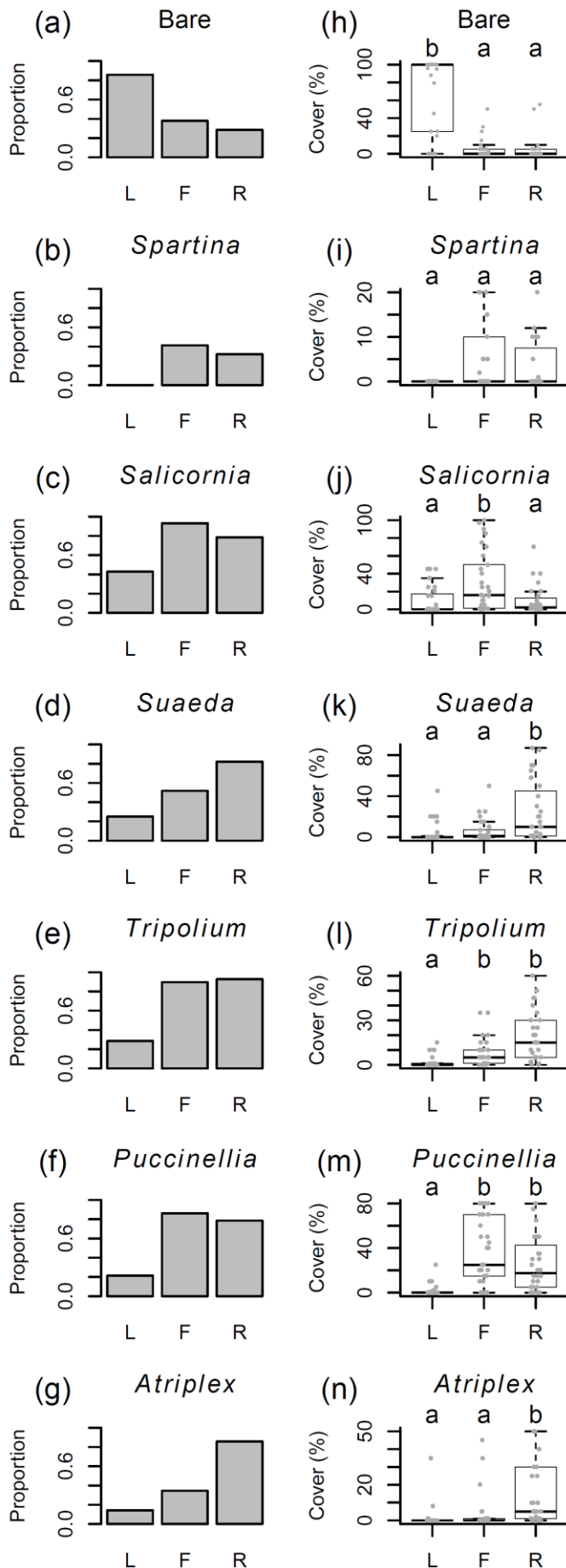


Fig. 2. (a-g) Proportion of unplanted plots with bare ground and the most abundant colonising species, and (h-n) percentage cover of bare ground and the most abundant colonising species. L=lowered, F=flat (level with marsh surface) and R= raised. Plots were sampled in October 2013, four growing seasons 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).

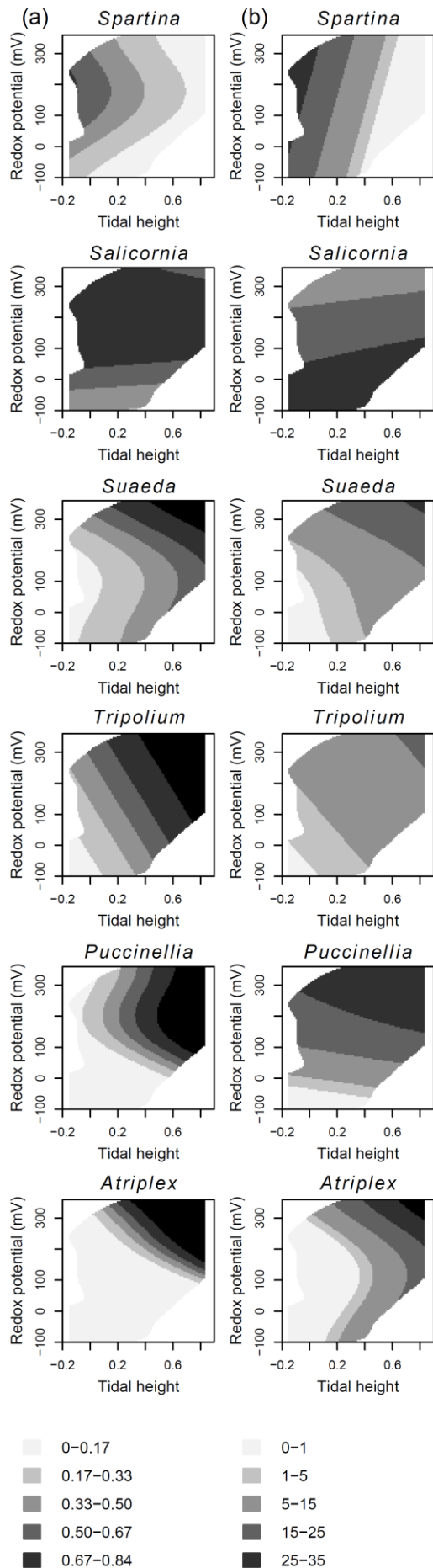


Fig. 3. Relationship between redox potential and tidal height and (a) the probability of occurrence and (b) the percentage cover (arcsine transformed) of the commonest species in unplanted plots.

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.

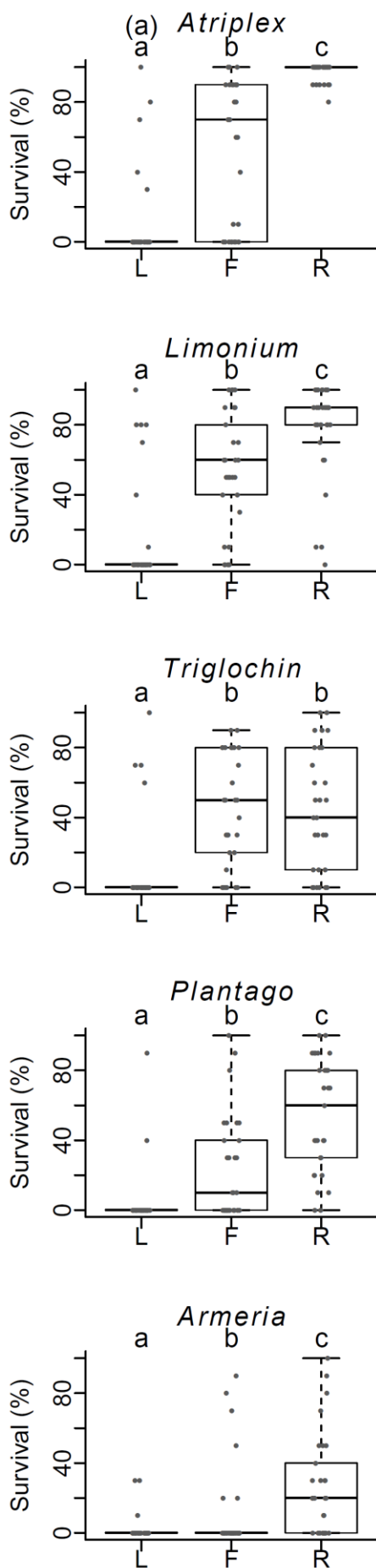


Fig. 4 Mean \pm SE proportion (%) of planted individual surviving in October 2013, 36-41 months after planting, in differing topographic treatments. L=lowered, F=level with marsh surface (control) and R= raised. Differing letters indicate significant differences between treatments (GLM $P < 0.001$, Tukey 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.

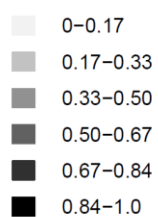
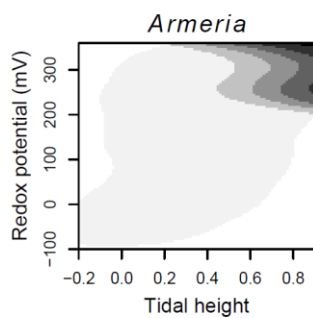
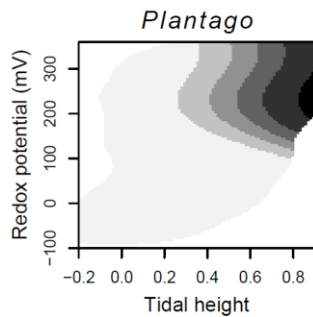
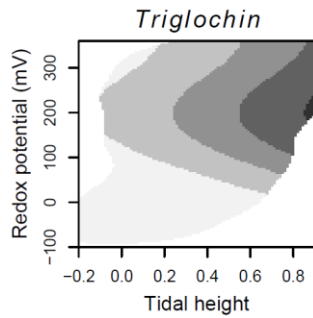
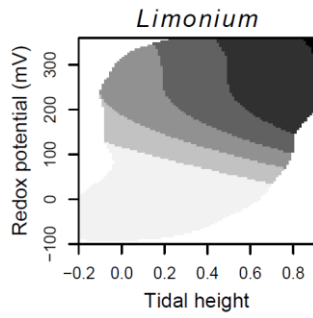
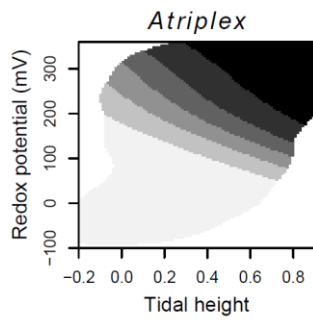


Fig. 5. Relationship between redox potential and tidal height and the proportion of surviving planted individuals in planted plots. Contours show the predicted probability from generalised additive models. Contour lines have been clipped to the area of data availability. Darker colours indicate higher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

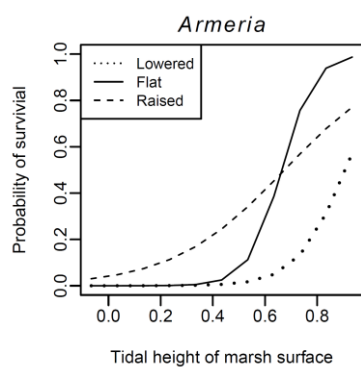
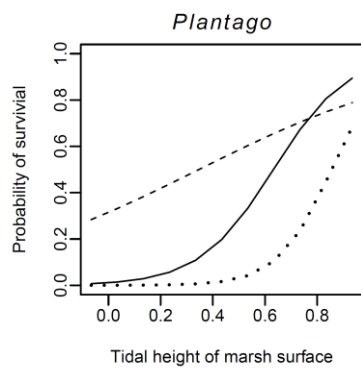
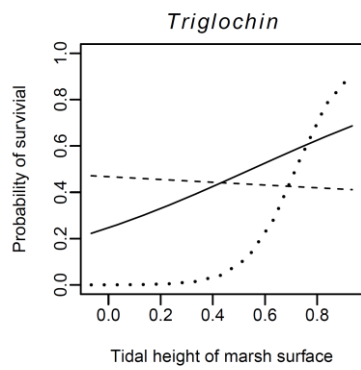
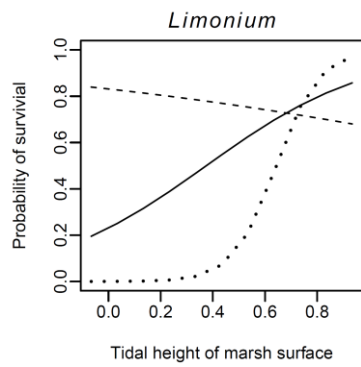
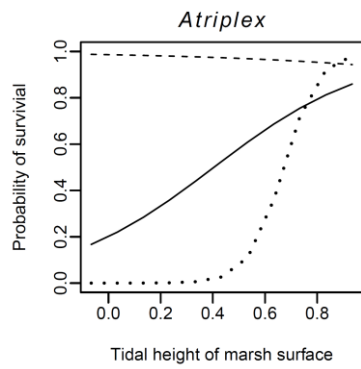


Fig. 6. Variation in the response to topographic manipulation treatment with elevation of marsh surface. Response curves are from generalised linear models of survival as a function of treatment and surrounding surface elevation, i.e. that of the flat plots, and the interaction between treatment and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

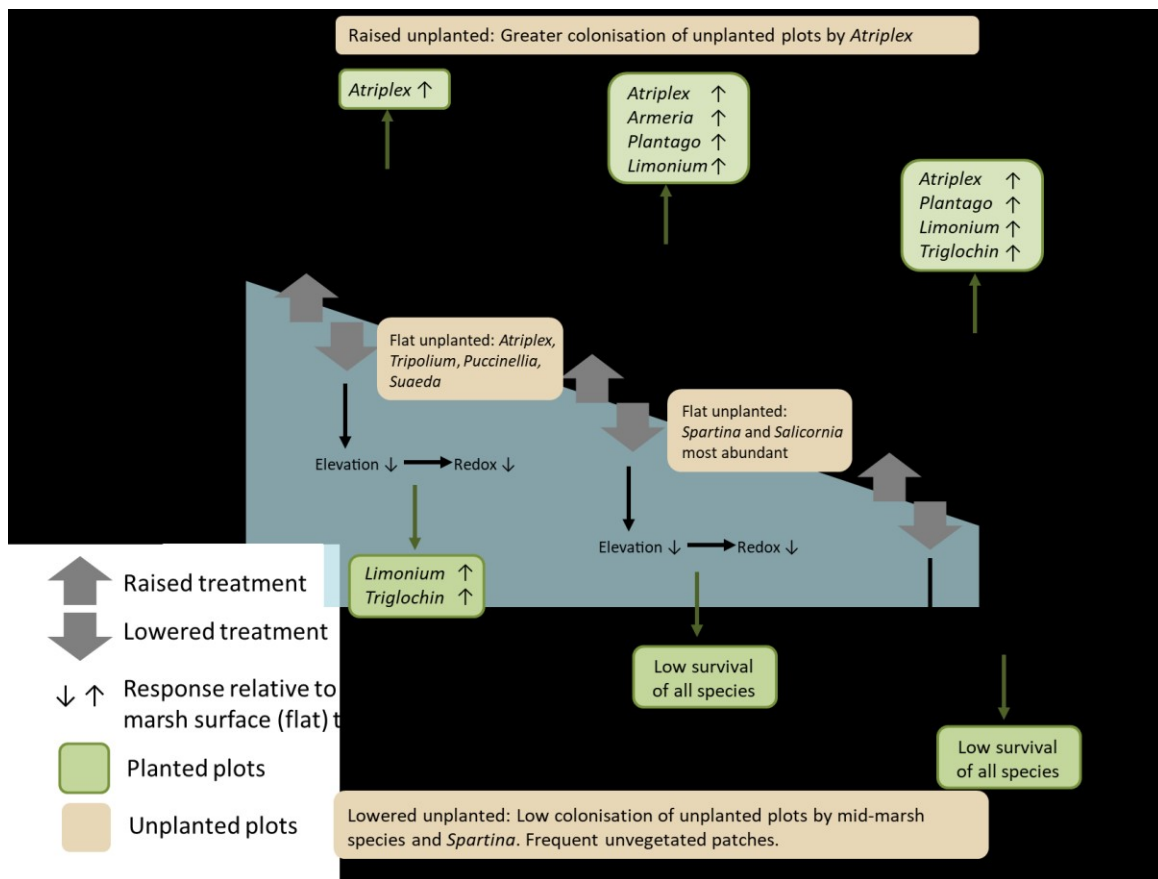


Fig. 7. Schematic diagram of how topographic manipulation (raising and lowering plots by ± 15 cm from the marsh surface) alters the elevation, redox potential and their relationship, and the consequences of this on plant survival and colonisation. Lowering plots reduces redox potential but the reduction 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.