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Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites?

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Summary

1. Coastal saltmarshes provide distinctive biodiversity and important ecosystem services, including coastal defence, supporting fisheries and nutrient cycling. However, *c*. 50% of the world's coastal marshes are degraded or have been lost, with losses continuing. In both Europe and North America, there is a legal requirement to create habitats to substitute for losses. How well do created habitats replicate natural salt marshes?

2. We compared plant communities and environmental characteristics of 18 deliberately realigned (managed realignment, MR - between 1 and 14 years old), 17 accidentally realigned (AR, 25–131 years old) sites with those on 34 natural reference saltmarshes in the UK.

3. Halophytic species colonized individual realignment sites rapidly, attaining species richness similar to nearby reference marshes after 1 year. Nevertheless, the community composition of MR sites was significantly different from reference sites, with early-successional species remaining dominant, even on the high marsh.

4. The dominance of pioneer species on the low and mid-marsh may be because, at the same elevation, sediments were less oxygenated than on reference sites. Sediments were well oxygenated on the high marsh, but were often drier than on natural marshes.

5. Overall community composition of AR marshes was not significantly different to reference marshes, but the characteristic perennials *Limonium vulgare*, *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* remained relatively rare. In contrast, the shrub *Atriplex portulacoides* was more abundant, and its growth form may inhibit or delay colonization by other species.

6. *Synthesis and applications*. Marshes created by managed realignment do not satisfy the requirements of the EU Habitats Directive. Adherence to the Directive might be improved by additional management interventions, such as manipulation of topographic heterogeneity or planting of mid- and upper-marsh species. However, given the inherent variation in natural saltmarshes and projected environmental change, policies that require exact equivalence at individual sites may be unachievable. More realistic goals might require minimum levels of a range of ecosystem functions on a broader scale, across catchments or regions.

Key-words: *Atriplex portulacoides*, dyke breach, habitat creation, managed retreat, redox potential, salt-marsh restoration, succession

Introduction

Global losses of coastal marsh have been and will continue to be extensive. Approximately 50% of saltmarsh area worldwide has already been lost or degraded (Adam 2002; Barbier *et al.* 2011). In recognition of the scale of habitat loss and the value of saltmarshes, there is considerable interest in reestablishing or creating saltmarsh covering the full range of habitats that have been lost. In the USA, section 404 of the Clean Water Act affords a high degree of protection to wetlands and has been interpreted as requiring 'no net loss' of both wetland area and function (Zedler 2004). Legislation in Europe seeks to

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maintain saltmarsh (and other natural habitats) in 'favourable status', including the maintenance of marsh area and the provision of compensatory habitat if areas are lost to development (European Commission 2000). Subsequent guidance from the EU has clarified that this means that 'a wetland should normally not be drained before a new wetland, with equivalent biological characteristics is available' and that 'the compensatory measures proposed for a project should address, in comparable proportions, the habitats and species negatively affected' (European Commission 2000).

There are various approaches to the creation of saltmarsh habitat, including plantings of ecosystem engineer species and the placement of dredged material. However, in the face of rising sea levels, managed coastal realignment has become an increasingly important option (French 2006). Despite numerous examples of such restoration, the extent to which they provide species and habitats in 'comparable proportions' to natural marshes is not clear. Nor do we know how long in advance of habitat loss the pre-emptive replacements need to be initiated. Many of the wetlands created to date in mitigation have not been equivalent to those destroyed (Race & Fonseca 1996; Turner, Redmond & Zedler 2001), and the speed with which natural saltmarsh structures and functions develop on restoration schemes has been highly variable. Halophytic species may colonize some newly restored saltmarshes quickly, and species richness may parallel reference areas within 7 years (Morgan & Short 2002; Mossman *et al.* 2012). At other sites, however, colonization has been slower (Onaindia, Albizu & Amezaga 2001; Wolters, Garbutt & Bakker 2005), and subsequent succession of plant communities may also be slow (Havens, Varnell & Watts 2002; Williams & Orr 2002). Differences in vegetation composition between natural and restored marshes have been detected after many decades (Burd, Clifton & Murphy 1994; Bakker 2002; Garbutt & Wolters 2008). Vegetation composition and physical structure inevitably have significant influences on saltmarsh ecosystem functions (Zedler, Callaway & Sullivan 2001; Doherty, Callaway & Zedler 2011), and large differences between the vegetation on restored and reference sites are likely to result in considerable disparity in ecosystem functioning.

Most of the deliberate reactivation (managed realignment) of saltmarsh sites has occurred within the last 20 years and therefore does not provide information to assess their equivalence in the long term. On the other hand, there are areas of saltmarsh that have developed after sea defences were accidentally breached during storm surges and remained unrepaired (Burd 1992; Burd, Clifton & Murphy 1994). In most cases, it has now been more than 50 years since tidal flow was restored to these accidentally realigned (AR) sites, and they can provide useful space-for-time analogues (Gray *et al.* 2002) for marsh development. On the basis of a survey of four deliberately restored marshes and 14 older accidentally flooded (AR) sites in the UK, each paired with one reference site, Garbutt & Wolters (2008) concluded that plant species richness was lower on restored sites and their plant communities different. This study, however, sampled only a small number of quadrats at each site and was focused on a restricted elevation range within the local tidal frame. Elevation is a major determinant of vegetation zonation and, consequently, of many ecosystem functions (e.g. Stagg & Mendelssohn 2010; Shepard, Crain & Beck 2011). In order to provide an adequate assessment of how well restored saltmarshes in the UK replicate reference marshes, we need to examine the whole elevation range of a site. The need to compare the attributes of restored sites to multiple reference sites is widely acknowledged (e.g. SER 2004), but few studies have done so. Furthermore, few studies of intertidal restorations have measured both biological and environmental attributes and, those that have, tend to be intensive studies of a single site (e.g. Spencer *et al.* 2008; Mossman *et al.* 2012).

In this study, we examine the vegetation that has developed on 18 deliberately realigned saltmarsh sites and 17 accidentally realigned sites, together ranging from 1 to 131 years since the restoration of tidal flow, and compare it with that of 34 reference saltmarshes. The aim was to assess the extent to which these realigned marshes have equivalent plant communities to natural reference marshes, and the time-scale for these to be established. It was expected that the vegetation of older realigned sites (25–131 years) would be more similar to the vegetation on reference sites than that on more recently realigned sites. Specific objectives were to (i) assess the colonization of halophytes with time since restoration, using a space-for-time substitution; (ii) compare species abundance and plant communities on realigned sites with those from reference marshes; and (iii) investigate environmental characteristics that may influence plant colonization and compare them with equivalent reference measurements.

Materials and methods

STUDY SITES

Sixteen saltmarshes reactivated through coastal managed realignment (MR), where sea defences have been relocated landward and the old, seaward wall breached to allow tidal inundation (French 2006), were selected. A further two sites reactivated by regulated tidal exchange (RTE) in England were selected; RTE differs from managed realignment in that tidal flooding enters the site through tidal gates or sluices, leaving the sea wall intact (hereafter RTE sites are included as MR). The 18 sites were selected to provide the maximum range of time since the restoration of tidal inundation (1–14 years). A further 17 accidentally realigned (AR) sites were selected for proximity to MR sites and to increase the range of time since the reintroduction of tidal inundation (25–131 years). The year in which tidal inundation was reactivated to each site was established from the literature (Burd 1992; Wolters, Garbutt & Bakker 2005) or from historical maps.

In addition to the realigned sites, 34 areas of 'natural' reference marsh were sampled, providing at least three reference marshes in proximity to each realigned site. Reference sites were selected for size (>2 ha), proximity to at least one realigned site and accessibility. The age of reference marshes is not known. The proximity of reference areas to realigned sites varied depending on the geomorphology of the estuary or coast. The distance between each realigned site and the nearest area of natural reference marsh (which was not necessarily sampled as a reference) was calculated from 1 : 25000 maps and measured from the centre of the realigned site. Details of all the sites are given in Table S1, Supporting Information.

There was no grazing by stock on any areas of the realigned sites studied. Three reference sites currently experience light, seasonal cattle grazing and three more reference sites, currently ungrazed, are known to have been grazed by stock in the past 20 years. It is likely that there is lagomorph and waterfowl grazing on most sites. There is also the possibility of deer grazing at some sites.

FIELD METHODS

Realigned and reference sites were each sampled once between July and October in 2004 and 2005, with the exception of Wallasea MR, which was sampled in 2010. Quadrats ($0{\cdot}5 \times 0{\cdot}5$ m) were located on transects spanning the elevation gradient at each site, with a minimum of two transects and 50 samples per site. The number of samples taken was proportional to the area of the site and to the distance from the upper strandline to mudflats in each case (numbers of samples given in Table S1, Supporting Information). Sampling points were located along transects positioned to ensure coverage of the whole elevation range at each site. Transects were started at random points along the landward edge of the marsh. In total, 900 quadrats were taken from MR sites, 850 from AR sites and 1950 from reference marshes.

At each quadrat, measurements were made of the vegetation, elevation above Ordnance Datum Newlyn (ODN, the UK terrestrial datum, *c.* mean sea level) and sediment redox potential; a sediment sample (*c.* 10 cm deep, 5 cm diameter) was collected and stored in a sealable polythene bag at 4 °C for laboratory analysis. All samples were taken at low tide, but it was not possible to restrict sampling to particular periods of the spring–neap cycle. Vegetation was assessed by recording percentage cover to the nearest 5% (rare species were assigned a value of 1%) of all vascular plant species. The area (%) of bare (unvegetated) ground in each quadrat was also recorded. Additional species not recorded in the quadrats but seen within 20 m of the transect were noted. Plant species nomenclature followed Stace (2010). The quadrat size was selected to minimize within-plot variation in environmental conditions. The elevation, relative to ODN, was measured at the centre of each quadrat using a differential GPS (Topcon, Newbury, UK), with a vertical accuracy of <2 cm and vertical precision of <2 cm. Substrate redox potential was measured at low tide with a single reading at 5 cm below the marsh surface taken from the centre of each quadrat using a BDH (British Drug Houses, Lutterworth, UK) Gelplas combination redox electrode with an Ag/AgCl reference, left until a stable reading was achieved (up to 5 min).

In the laboratory, a subset of unsieved sediment samples (45–55% of the collections for each site) was selected haphazardly. Duplicate subsamples (*c.* 5 g of each substrate sample) were oven-dried (16 h at 90 °C) to determine gravimetric sediment water content and then ignited in a muffle furnace (16 h at 390 °C) to determine organic matter content (loss on ignition). The mean of the duplicates was used in statistical analyses.

ELEVATION IN RELATION TO THE TIDAL FRAME

Elevation of quadrats was measured relative to ODN, but in order to compare quadrats from different sites, the elevations needed to be considered relative to the local tidal regime (Mossman, Davy & Grant 2012). A subset of six MR, four AR and eight reference sites was selected for which on-site measurements of tidal regime had been made (Mossman, Davy & Grant 2012; H.L. Mossman unpublished data). A further three MR, three AR and 10 reference sites were included because they were situated close to a port for which tidal data were available, and the port and the site were in a relatively simple geomorphological setting. For each of these 34 sites, the levels of mean high water neap (MHWN) and mean high water spring (MHWS) tides were determined. These were used to calculate relative tidal height on a scale where 0 = MHWN, 1 = MHWS, using:

Relative tidal height = Elevation relative to ODN – MHWN/(MHWS-MHWN).

DATA ANALYSIS

The species compositions of realigned and reference sites were compared to a species pool defined as all salt-tolerant species recorded during the study; species with Ellenberg salinity values of 0 or 1 were excluded because these species are intolerant or only slightly tolerant of saline conditions (Hill, Preston & Roy 2004). The fraction of the species pool occurring on realigned sites was correlated with both the time since restoration of tidal inundation and distance from the nearest area of reference marsh using Spearman's rank correlation; similarly, correlations between plant cover and time since restoration were investigated. Simpson's diversity index was calculated for each quadrat and compared between MR, AR and reference marshes using Mann–Whitney *U*-tests, adjusted for multiple comparisons using the Bonferroni correction.

Samples from individual sites were grouped by marsh types into MR, AR and reference marsh data sets. Multi-dimensional scaling (MDS) and permutation tests (ANOSIM), using Bray–Curtis similarity index, were used to examine and test the statistical significance of differences in plant communities between marsh types (Clarke & Green 1988).

Sediment redox potential, water content and organic content and tidal height were compared between marsh types using Mann–Whitney *U*-tests. LOESS (locally weighted scatterplot smoothing) regressions (Cleveland & Devlin 1988) were fitted to tidal height and sediment redox potential using the standard package of R. This fits a smooth, but not necessarily monotonic, relationship to the data using a procedure similar to calculating a moving average. Samples for which tidal regime data were available were divided into three tidal elevation groups with equal numbers of quadrats; low (<0·65), mid (0·65–0·90) and high (>0·90). The abundance (cover) of the eleven most common plant species and of bare ground within tidal elevation groups was compared between marsh types using Mann–Whitney *U*-tests, adjusted for multiple comparisons using the Bonferroni correction.

Data were analysed using SPSS 16.0 (SPSS Inc, Chicago, IL, USA), Primer 6.0 (Primer-E, Plymouth, UK) and R 2.10.1 (R Development Core Team 2008).

Results

DEVELOPMENT OF PLANT SPECIES DIVERSITY

Salt-marsh plant species colonized realigned sites quickly following the restoration of tidal inundation, as sites only 1-year old had a similar fraction of pool species to that on older realigned sites, and all percentages were within or close to the range found on reference marshes (Fig. 1). The fraction of the species pool occurring at each site was highly variable between reference marshes and between realigned sites of the same age (Fig. 1). There was no correlation between time since restoration and the fraction of pool species found on realigned sites ($r_s = -0{\cdot}082$, $P = 0{\cdot}641$, $n = 35$).

Several plant species frequently found on the reference marshes were found on a smaller proportion of MR sites, for example, *Atriplex portulacoides*, *Limonium vulgare* and *Armeria maritima* (Table 1). In contrast, *Atriplex portulacoides* and *Limonium vulgare* occurred frequently on AR sites. Although *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* occurred on a greater proportion of older realigned sites (AR) compared to younger (MR) sites, these species were absent more frequently than on reference marshes (Table 1).

Sixty-five per cent of MR sites and 73% of AR sites were adjacent to areas of natural saltmarsh, and only two realigned sites were further than 5 km from an area of natural marsh. No correlation was found between the distance from realigned sites to the nearest area of natural marsh and the fraction of the species pool occurring on the site ($r_s = -0{\cdot}241$, $P = 0{\cdot}163$). There was also no relationship between distance and the fraction of the species pool occurring on the site if MR sites were considered separately ($r_s = -0{\cdot}315$, $P = 0{\cdot}203$).

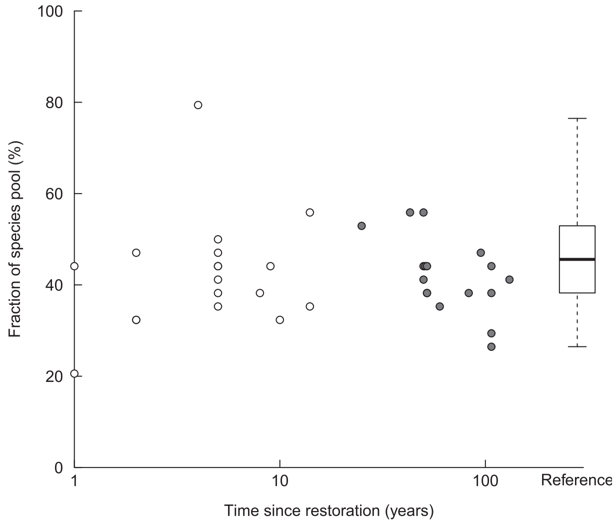

Fig. 1. Fraction of pool species that have colonized realigned saltmarshes in relation to the time since restoration; managed realignment sites (open circles), accidentally realigned sites (filled circles). The percentage of species found on reference sites is also shown as a box plot ($n = 34$). Species pool is defined as the total number of salt-tolerant species (Ellenberg salinity value >1) recorded during this study.

Table 1. Percentage of managed realignment (MR, $n = 18$), accidentally realigned (AR, $n = 17$) and reference ($n = 34$) sites on which the 15 species most commonly present on reference marshes occur

	MR	AR	Reference
Aster tripolium	94	100	100
Puccinellia maritima	94	100	100
Spartina anglica	78	93	97
Spergularia media	83	87	97
Salicornia europaea	94	100	94
Triglochin maritima	44	73	92
Atriplex portulacoides	67	100	89
Cochlearia spp.	61	80	89
Elytrigia atherica	83	80	89
Suaeda maritima	89	100	83
Plantago maritima	50	47	83
Limonium vulgare	39	93	81
Festuca rubra	56	20	67
Armeria maritima	11	27	53
Sarcocornia perennis	50	73	44

Species diversity (Simpson's index) was significantly lower in quadrats from MR sites (median, 25–75th percentiles: 0·43, 0·13–0·58) compared to those from reference marshes (0·53, 0·35–0·67; $Z = 6{\cdot}100$, $P < 0{\cdot}001$) and AR sites (0·48, 0·27–0·60; $Z = 2{\cdot}472$, $P = 0{\cdot}013$). Samples from AR sites also had lower diversity than those from reference sites ($Z = 3{\cdot}135$, $P = 0{\cdot}002$). The vegetation in the majority of quadrats from MR sites comprised a subset of communities present on natural reference marshes (Fig. 2) and, overall, was significantly different (ANOSIM) to that from natural reference ($R = 0{\cdot}151$, $P = 0{\cdot}001$) and AR sites ($R = 0{\cdot}152$, $P = 0{\cdot}001$). There was no significant difference in plant communities between AR and reference sites ($R = -0{\cdot}003$, $P = 0{\cdot}694$). Overall, MR sites had significantly more bare ground than natural reference marshes ($Z = -3{\cdot}75$, $P < 0{\cdot}001$), but the coverage of bare ground decreased with increasing time since tidal restoration (Fig. 3). The abundance (cover) of *Spartina anglica*, *Salicornia europaea*, *Atriplex portulacoides*, *Limonium vulgare* and *Puccinellia maritima* increased with time since restoration (Fig. 3). The abundance of other species did not increase significantly with time since restoration.

PLANT COMMUNITIES IN RELATION TO THE TIDAL FRAME

To investigate whether the observed differences in vegetation were because of differences in elevation, we examined a subset of nine MR sites, seven AR sites and 18 reference

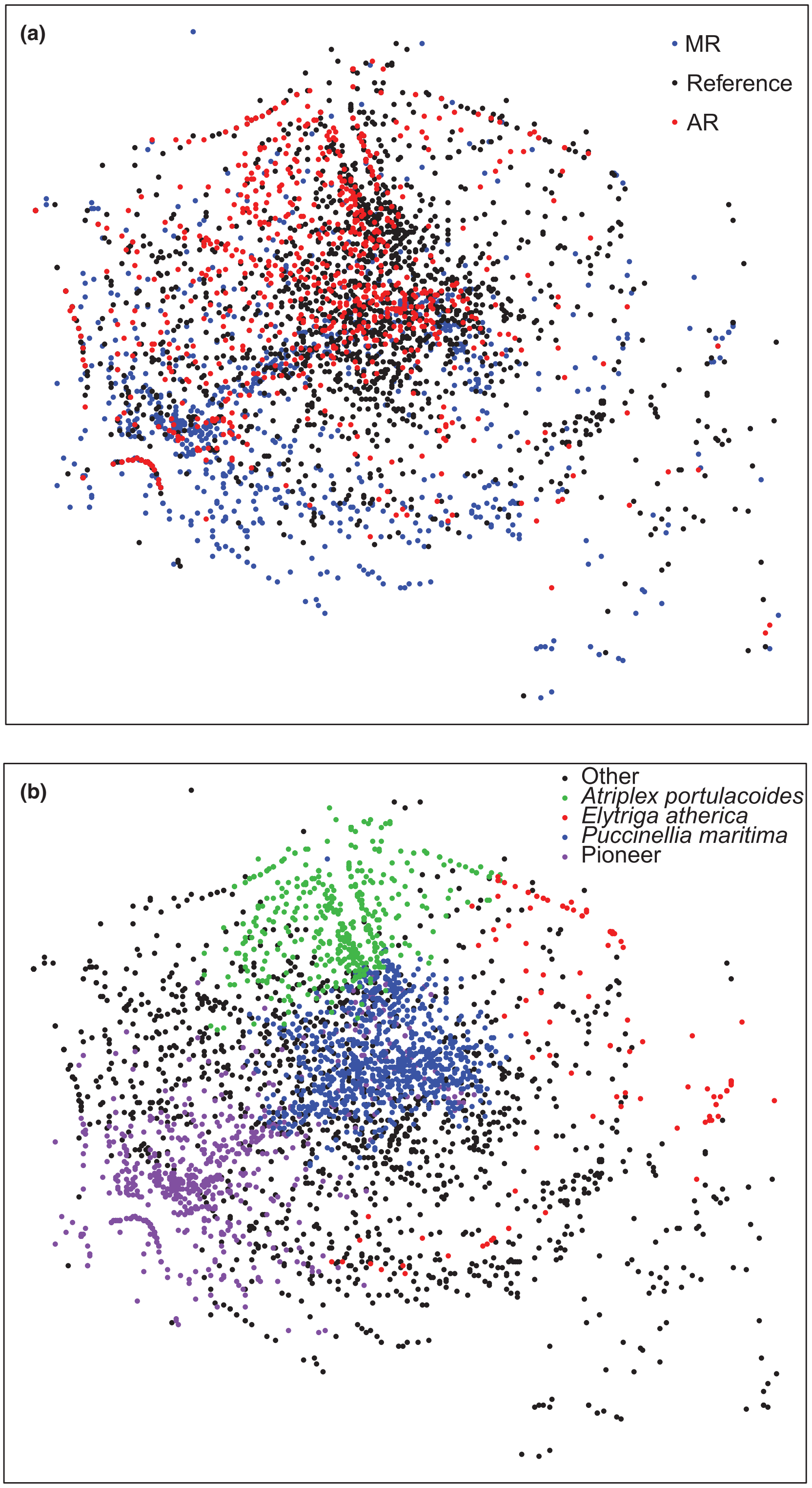

Fig. 2. Non-metric multi-dimensional scaling ordination of vegetation in quadrats from reference and realigned saltmarshes. The similarity in species composition of individual quadrats is represented by their spatial proximity. (a) Distribution of quadrats from managed realignment sites (MR, $n = 900$), older, accidentally realigned marshes (AR, $n = 850$) and reference marshes ($n = 1950$); (b) Distribution of dominant plant species (cover >50%) in the quadrats, Pioneer is defined as having cover of bare ground and/or *Salicornia europaea* >50%). Stress = 0·17.

sites for which data were available on the relationship between elevation above ODN and tidal inundation.

Overall, quadrats from MR and AR sites were significantly lower in the tidal frame than those from reference sites ($Z = -9{\cdot}98$, $P < 0{\cdot}001$; $Z = -5{\cdot}669$, $P < 0{\cdot}001$, respectively). However, there were differences between MR and reference sites in the abundance of plant species at all elevations (Fig. 4). Quadrats from MR sites were significantly less vegetated at all elevations compared to those from reference sites (Fig. 4). Plant communities at mid-marsh elevations on reference and AR sites were dominated by *Puccinellia maritima* and *Atriplex portulacoides*. However, at mid-marsh elevations, MR sites had much bare ground and significantly greater coverage of the pioneer annuals, *Salicornia europaea* and *Suaeda maritima*. *Limonium vulgare*, *Armeria maritima*, *Triglochin*

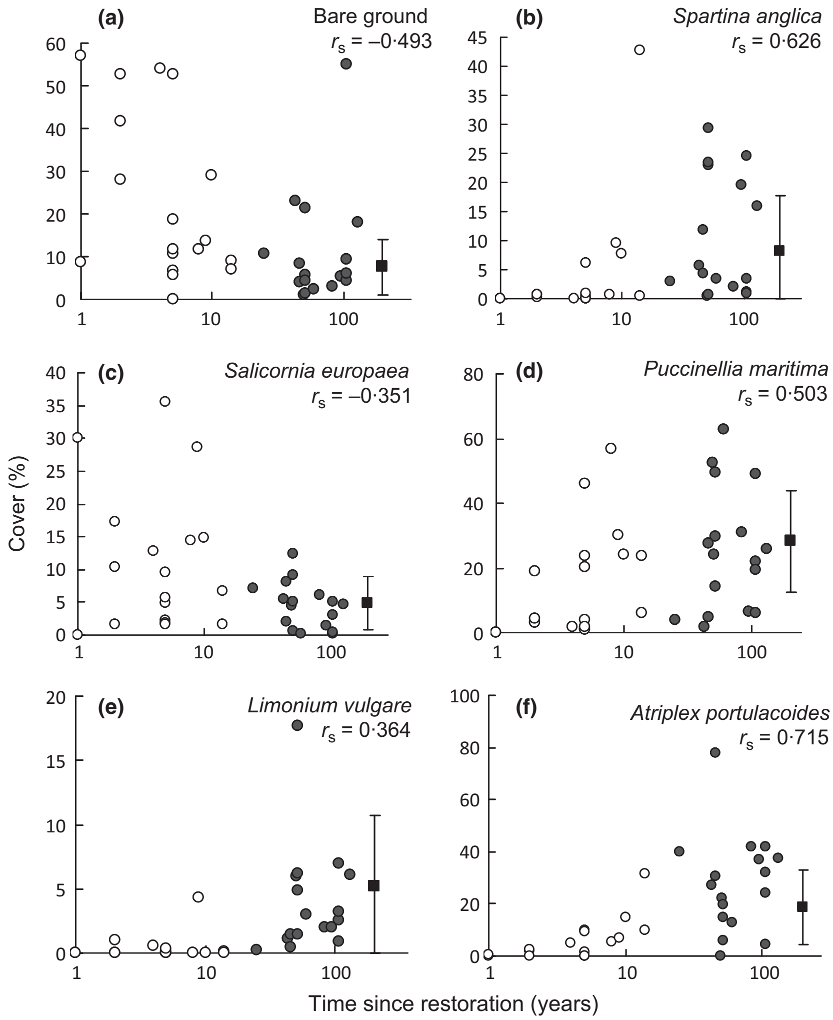

Fig. 3. Cover (%) of bare ground and five saltmarsh plant species on realigned saltmarshes in relation to the time since restoration; managed realignment sites (open circles), accidentally realigned sites (filled circles). All correlations, $P < 0{\cdot}05$. The mean (± SD) cover on reference marshes (filled square, n = 34) is also shown.

maritima and *Plantago maritima* were relatively abundant at mid- and high elevations on reference marshes, but were less abundant on realigned sites.

ENVIRONMENTAL CHARACTERISTICS

Redox potential increased with increasing elevation in the tidal frame ($r^2 = 0{\cdot}351$, $P < 0{\cdot}001$). However, the relationship between redox potential and elevation differed between MR, AR and reference samples (Fig. 5a). Redox potentials of samples from AR sites were on average lower than those from reference sites regardless of tidal height and overall were significantly lower than those from reference sites (Fig. 5b; $Z = 7{\cdot}859$, $P < 0{\cdot}001$). While the redox potentials of samples from MR sites were significantly lower than those from reference sites (Fig. 5b; $Z = 3{\cdot}590$, $P < 0{\cdot}001$), this was not simply because reference sites were higher in the tidal frame. Below a relative tidal height of 0·75, the redox potentials of MR samples were on average lower than those on reference sites, but MR samples above a tidal height of 0·75 had higher redox potentials than those on reference marshes (Fig. 5a). Sediments of MR samples from elevations in the tidal frame of > 0·75 were significantly drier ($Z = 8{\cdot}188$, $P < 0{\cdot}001$) and contained significantly less organic matter ($Z = 5{\cdot}746$, $P = 0{\cdot}001$) than samples from reference marshes (Fig. 6).

Discussion

The establishment of saltmarsh through managed realignment has often been described as successful (e.g. Boorman, Hazelden & Boorman 2002; Spencer *et al.* 2008). Our work only agreed with this in so far as typical halophytic plant species quickly colonized MR sites. Garbutt & Wolters (2008) found that species richness was lower on 72% of restored sites compared to a paired reference marsh. However, species richness was highly variable between the reference marshes studied by Garbutt & Wolters (2008), and the species richness of 77% of the restored marshes was within the range of reference marshes. High variability can both mask differences between restored and natural sites (Neckles *et al.* 2002) and impede the identification of developmental trajectories (Simenstad & Thom 1996). This highlights the importance of comparing restored sites to at least two reference sites (Ruiz-Jaen & Aide 2005) and setting restoration tar-

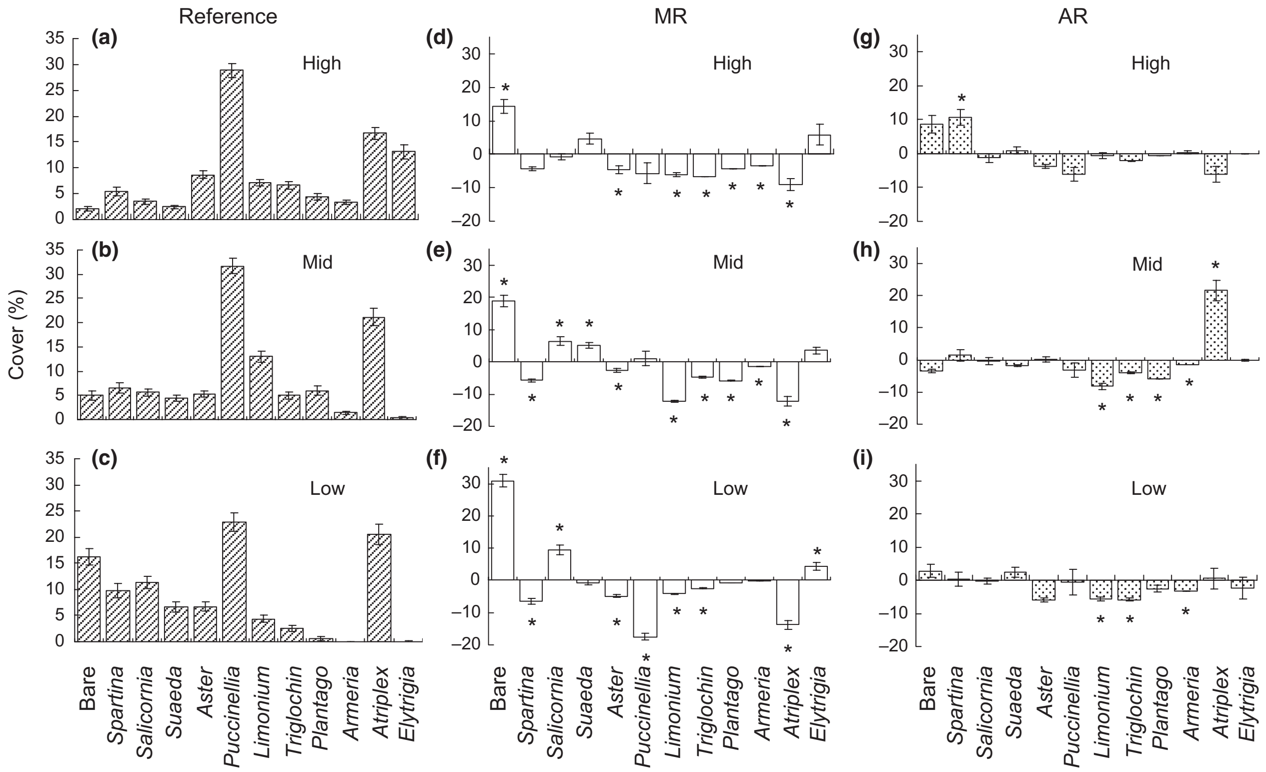

Fig. 4. Mean (± SE) cover (%) of the eleven most frequently recorded plant species and bare ground on reference saltmarsh samples from (a) high-, (b) mid- and (c) low-marsh elevations (hatched, $n = 34$). Differences from the mean cover of reference sites in samples from managed realignment (MR, unshaded; d, e, f; $n = 18$) and accidentally realigned (AR, stippled; g, h, i; $n = 17$) sites. An asterisk indicates cover that is significantly different ($P < 0{\cdot}05$) from that on reference marshes.

gets that allow for between-site variability (Short *et al.* 2000).

While the species richness of whole realigned sites was similar to that of reference sites, plant communities in individual quadrats on MR sites were certainly not equivalent. There was more bare ground on MR sites, and species characteristics of pioneer and low saltmarsh, such as *Salicornia europaea* (Davy, Bishop & Costa 2001) and *Puccinellia maritima* (Gray & Scott 1977), were most abundant. In the low-lying areas of some MR marshes, limited vegetation cover and dominance of pioneer species could be a result of bioturbation by invertebrate infauna (Paramor & Hughes 2005), or it may simply indicate an early-successional state.

Our environmental data, however, indicate a more fundamental reason for these vegetational differences on the low marsh. Sediment conditions in lower-lying areas of realigned marshes were less oxygenated than those at corresponding elevations of reference marshes. Sediment redox potential has effects on plant abundance, independently from elevation (Davy *et al.* 2011), and low redox potential may inhibit vegetation colonization or limit colonization to species tolerant of waterlogged conditions (Mossman *et al.* 2012). The less oxygenated sediment conditions of low- and mid-marsh elevations on newly realigned sites thus shift the vegetation towards more inundation-tolerant, pioneer communities. Studies that assess the success of saltmarsh restoration by comparing the species composition of paired reference and restored samples of the same elevation may therefore exaggerate the differences in species abundance between restored and reference samples.

In contrast, at higher elevations, sediments of MR sites were better oxygenated but nevertheless remained significantly less vegetated. These sediments were drier and contained less organic matter than those from the same elevations on reference marshes. These areas may remain sparsely vegetated because patches of bare sediments on the high marsh are frequently hypersaline as a result of high surface evaporation and infrequent tidal inundation (Bertness 1991; Bertness, Gough & Shumway 1992). The initial surface elevation at an MR site depends, among other things, on the period of reclamation for agricultural use before restoration, during which there will have been shrinkage and consolidation of the sediments (Crooks *et al.* 2002).

Atriplex portulacoides, potentially the physiognomic dominant on marshes around much of the European coastline, was significantly more abundant on older realigned marshes than on reference sites, and it is rapidly increasing in dominance at several MR sites (e.g. Freiston Shore (H.L. Mossman, *pers obs*). *Atriplex portulacoides* is intolerant of waterlogging (Davy *et al.* 2011), particularly at the seedling stage (Chapman 1950) and is therefore not

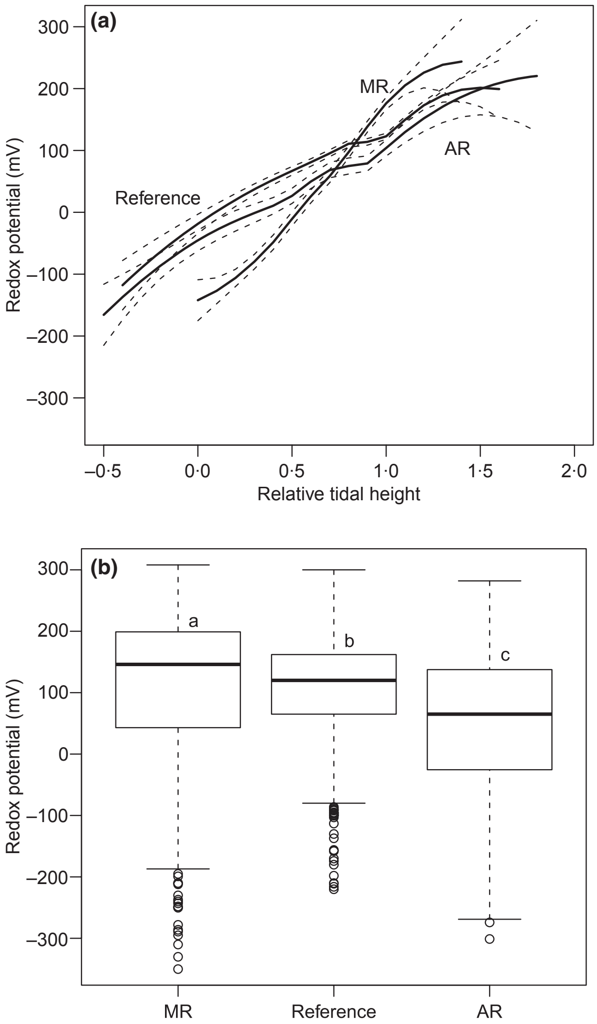

Fig. 5. (a) LOESS regressions (±SE) of the relationship between redox potential and elevation in the tidal frame (scaled from 0 (MHWN) to 1 (MHWS) at sampling locations on managed realignment (MR, n = 450), accidentally realigned (AR, n = 350) and reference saltmarshes (n = 990). (b) Box plots of redox potential of samples from managed realignment (n = 800), accidently realigned (n = 850) and reference saltmarshes (n = 1800). Different letters indicate significant differences (P < 0·005).

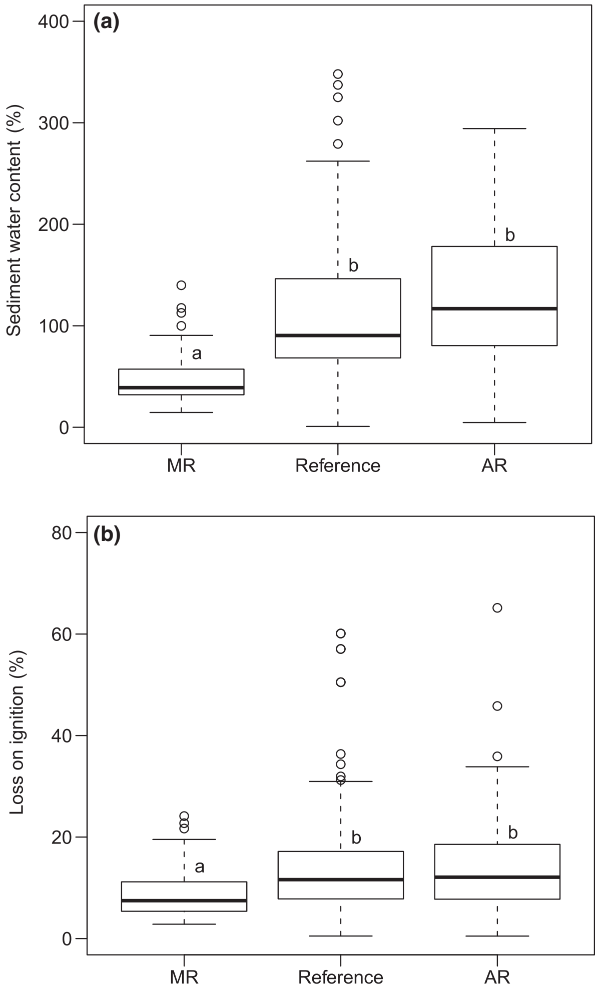

Fig. 6. (a) Sediment water content and (b) sediment organic matter (loss on ignition) of samples from elevations in the tidal frame of higher than 0·75 at managed realignment (MR, n = 178), accidentally realigned (AR, n = 110) and reference saltmarshes (n = 205). Different letters indicate significant differences (P < 0·005).

an early colonist of naturally accreting and establishing marshes. However, areas of some managed realignment sites are at elevations in the tidal frame that have suitable sediment conditions for its colonization immediately following reinstatement of tidal flow. In these areas, facilitated succession is not necessary. Species that are quick to colonize, and that are both fast growing and long-lived, may become dominant by inhibiting the invasion of subsequent colonists for as long as they persist (inhibition succession; Connell & Slatyer 1977). *Atriplex portulacoides* is a long-lived perennial shrub (Chapman 1950). While few individuals have been observed colonizing mature, dense saltmarsh swards (Mohamed 1998), individuals of *A. portulacoides* can produce very large numbers of fruits, and germination rates can be high (Mohamed 1998). The establishment of species such as *Armeria maritima* on to realigned sites may be inhibited by the rapid growth and subsequent dominance of *Atriplex portulacoides*, with opportunities for recruitment of rarer species limited to disturbance events. Our study sites were biased towards the southern UK in which species of predominantly southern distribution, such as *Limonium vulgare* and *Atriplex portulacoides*, are prominent, but the general principles should be widely applicable.

Although distance from the nearest potential propagule source was not related to species richness on realigned marshes in this study, low seed viability and long reproductive cycles of *Limonium vulgare*, *Triglochin maritima* and *Plantago maritima* (Boorman 1967; Hutchings & Russell 1989; Davy & Bishop 1991) may slow the ability of these species to colonize and spread within newly realigned marshes. Propagule addition or the transplantation of rarer species on to newly restored sites may increase their frequency in the longer term (Armitage *et al.* 2006; Varty & Zedler 2008). The creation of small-scale heterogeneity of edaphic conditions may also provide refuges for rarer species (Ewanchuk & Bertness 2004; Varty & Zedler 2008).

To what extent are the restored marshes likely to provide similar ecosystem functions to reference marshes? As we have not measured functions, we do not know how relatively small differences in plant communities might translate into important differences in ecosystem functions and services. A large meta-analysis of wetland restoration suggested that structural recovery may be necessary to achieve functional recovery (Moreno-Mateos *et al.* 2012). However, equivalent vegetation composition does not guarantee functional equivalency (Zedler & Lindig-Cisneros 2000), so it is unlikely that restored marshes with very different vegetation will be functionally equivalent. Floristic differences on saltmarshes have been associated with substantial functional differences. For example, the dominant plant species in a saltmarsh community has a major influence on metrics of productivity and nitrogen accumulation (Sullivan, Callaway & Zedler 2007; Doherty, Callaway & Zedler 2011). The plants that occur at a particular location are indicative of the redox status of the soil (Davy *et al.* 2011), and low redox is associated with increased greenhouse gas emissions (Ding, Zhang & Cai 2010; Adams, Andrews & Jickells 2012). Sparse vegetation is likely to result in lower wave energy attenuation (Möller *et al.* 2001) and lower productivity, whereas areas where the evergreen shrub *Atriplex portulacoides* is dominant may be more effective in protecting sea walls from wave action. Dominance of species such as *Atriplex portulacoides* may further affect functioning by inhibiting colonization by less common species that perform differing functions (Zedler, Callaway & Sullivan 2001). Lower abundance of plant species such as *Limonium vulgare* on realigned marshes will reduce faunal biodiversity, as many invertebrate species are exclusively dependent on these plants (Agassiz *et al.* 2000). As *Limonium vulgare* and *Armeria maritima* flower in summer, when visitor use of marshes is at its highest, their low abundance will reduce the aesthetic and recreational value of created marshes.

While the vegetation of realigned marshes was more similar to reference marshes after 50 or 100 years, some differences in species abundance and diversity remained. This may be related to the relatively high floristic diversity of these marshes; studies of much less diverse North American Atlantic saltmarshes suggest vegetation cover or species richness can reach equivalence within 10 years (LaSalle, Landin & Sims 1991; Morgan & Short 2002). However, vegetation structure expressed as stem density (Zedler 1993), and ecosystem functions, such as carbon burial (Craft *et al.* 1999; Morgan & Short 2002), may take decades to reach equivalence. We have only examined sites resulting from coastal realignment, but it is likely that marshes restored by other approaches would exhibit similar properties in areas of high floristic diversity. Even where an ecosystem engineer, such as *Spartina maritima*, is planted extensively, high-marsh development may still depend on subsequent successional processes (Castillo & Figueroa 2009).

It is clear from our work that marshes reactivated by managed realignment do not provide habitats and species in comparable proportions to natural marshes and do not have equivalent biological characteristics. They therefore do not satisfy the requirements of the EU Habitats Directive. It may be possible to improve adherence to the Directive in the future. Additional management interventions, such as the creation of topographic heterogeneity and the planting of mid- and upper-marsh species, could accelerate convergence. On the other hand, given the inherent variation in both natural saltmarshes and local responses to realignment, in the context of projected sea-level rise and climatic change, exact equivalence at individual sites may not be feasible. The requirements of the US Clean Water Act may be more achievable, if implemented by requiring minimum levels of a range of ecosystem functions, and no net loss on larger spatial scales. Nevertheless, a focus on ecosystem functions must not obscure the fact that we do not yet know how to create saltmarshes similar to the flower-rich 'general saltmarsh' characteristic of the upper parts of natural marshes and sites with these characteristics merit even higher protection. Planned MR schemes should include measures to encourage the development of these communities, so that we maintain the full range of habitats and species across catchments and regions, even if this is not achieved at every individual site.

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References

Adam, P. (2002) Salt marshes in a time of change. *Environmental Conservation*, **29**, 39–61.

Adams, C.A., Andrews, J.E. & Jickells, T. (2012) Nitrous oxide and methane fluxes vs. carbon, nitrogen and phosphorous burial in new intertidal and saltmarsh sediments. *Science of the Total Environment*, **434**, 240–251.

Agassiz, D.J.L. (2000) Lepidoptera of British saltmarshes. *British Saltmarshes* (eds B.R. Sherwood, B.G. Gardiner & T. Harris), pp. 303–308. Linnean Society of London/Forrest Text, London, UK.

Armitage, A.R., Boyer, K.E., Vance, R.R. & Ambrose, R.F. (2006) Restoring assemblages of salt marsh halophytes in the presence of a rapidly colonizing dominant species. *Wetlands*, **26**, 667–676.

Bakker, J.P. (2002) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29–51.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, **81**, 169–193.

Bertness, M.D. (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology*, **72**, 125–137.

Bertness, M.D., Gough, L. & Shumway, S.W. (1992) Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology*, **73**, 1842–1851.

Boorman, L.A. (1967) Biological flora of the British Isles *Limonium vulgare* Mill. and *L. humile* Mill. *Journal of Ecology*, **55**, 221–232.

Boorman, L., Hazelden, J. & Boorman, M. (2002) New salt marshes for old – salt marsh creation and management. Littoral 2002, The Changing Coast. Porto, Portugal.

Burd, F. (1992) *Historical Study of Sites of Natural Sea Wall Failures in Essex*. University of Hull, Institute of Estuarine and Coastal Studies, Hull, UK.

Burd, F., Clifton, J. & Murphy, B. (1994) *Sites of Historical Sea Defence Failure. Phase II study*. Institute of Estuarine and Coastal Studies, Hull, UK.

Castillo, J.M. & Figueroa, E. (2009) Restoring salt marshes using small cordgrass, *Spartina maritima*. *Restoration Ecology*, **17**, 324–326.

Chapman, V.J. (1950) Biological flora of the British Isles: *Halimione portulacoides* (L.) Aell. *Journal of Ecology*, **38**, 214–222.

Clarke, K.R. & Green, R.H. (1988) Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series*, **46**, 213–226.

Cleveland, W.S. & Devlin, S.J. (1988) Locally-weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, **83**, 596–610.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *The American Naturalist*, **111**, 1119–1144.

Craft, C., Reader, J., Sacco, J.N. & Broome, S.W. (1999) Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications*, **9**, 1405–1419.

Crooks, S., Schutten, J., Sheern, G.D., Pye, K. & Davy, A.J. (2002) Drainage and elevation as factors in the restoration of salt marsh in Britain. *Restoration Ecology*, **10**, 591–602.

Davy, A.J. & Bishop, G.F. (1991) Biological flora of the British Isles: *Triglochin maritima* L. *Journal of Ecology*, **79**, 531–555.

Davy, A.J., Bishop, G.F. & Costa, C.S.B. (2001) Biological flora of the British Isles: *Salicornia* L. (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea L., S. obscura* P.W. Ball & Tutin, *S. nitens* P.W. Ball & Tutin, *S. fragilis* P.W. Ball & Tutin and *S. dolichostachya* Moss). *Journal of Ecology*, **89**, 681–707.

Davy, A.J., Brown, M.J.H., Mossman, H.L. & Grant, A. (2011) Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. *Journal of Ecology*, **99**, 1350–1357.

Ding, W., Zhang, Y. & Cai, Z. (2010) Impact of permanent inundation on methane emissions from a *Spartina alterniflora* coastal salt marsh. *Atmospheric Environment*, **44**, 3894–3900.

Doherty, J.M., Callaway, J.C. & Zedler, J.B. (2011) Diversity–function relationships changed in a long-term restoration experiment. *Ecological Applications*, **21**, 2143–2155.

European Commission (2000) *Managing Natura 2000 Sites: The Provisions of Article 6 of the 'Habitats' Directive 92/43/EEC*. Office for Official Publications of the European Communities, Luxembourg, pp. 66.

Ewanchuk, P.J. & Bertness, M.D. (2004) The role of waterlogging in maintaining forb pannes in northern New England salt marshes. *Ecology*, **85**, 1568–1574.

French, P.W. (2006) Managed realignment – The developing story of a comparatively new approach to soft engineering. *Estuarine Coastal and Shelf Science*, **67**, 409–423.

Garbutt, A. & Wolters, M. (2008) The natural regeneration of salt marsh on formerly reclaimed land. *Applied Vegetation Science*, **11**, 335–344.

Gray, A.J. & Scott, R. (1977) The ecology of Morecambe Bay. VII. The distribution of *Puccinellia maritima, Festuca rubra* and *Agrostis stolonifera* in salt marshes. *Journal of Applied Ecology*, **14**, 229–241.

Gray, A., Simenstad, C.A., Bottom, D.L. & Cornwell, T.J. (2002) Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River estuary, Oregon, USA. *Restoration Ecology*, **10**, 514–526.

Havens, K.J., Varnell, L.M. & Watts, B.D. (2002) Maturation of a constructed tidal marsh relative to two natural reference tidal marshes over 12 years. *Ecological Engineering*, **18**, 305–315.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT - Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology and Hydrology, Huntingdon, UK.

Hutchings, M.J. & Russell, P.J. (1989) The seed regeneration dynamics of an emergent salt marsh. *Journal of Ecology*, **77**, 615–637.

LaSalle, M.W., Landin, M.C. & Sims, J.G. (1991) Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. *Wetlands*, **11**, 191–208.

Mohamed, M.F. (1998) Ecological Studies on *Atriplex portulacoides* and its Role in Saltmarsh Zonation. Unpublished PhD thesis, University of East Anglia, Norwich, UK.

Möller, I., Spencer, T., French, J.R., Leggett, D.J. & Dixon, M. (2001) The sea-defence value of salt marshes – a review in the light of field evidence from North Norfolk. *Journal of the Chartered Institution of Water and Environmental Management*, **15**, 109–116.

Moreno-Mateos, D., Power, M.E., Comin, F.A. & Yockteng, R. (2012) Structural and functional loss in restored wetland ecosystems. *Plos Biology*, **10**, e1001247. doi:10.1371/journal.pbio.1001247.

Morgan, P.A. & Short, F.T. (2002) Using functional trajectories to track constructed salt marsh development in the Great Bay estuary, Maine/New Hampshire, U.S.A. *Restoration Ecology*, **10**, 461–473.

Mossman, H.L., Davy, A.J. & Grant, A. (2012) Quantifying local variation in tidal regime using depth-logging fish tags. *Estuarine Coastal and Shelf Science*, **96**, 122–128.

Mossman, H.L., Brown, M.J.H., Davy, A.J. & Grant, A. (2012) Constraints on salt marsh development following managed coastal realignment: dispersal limitation or environmental tolerance? *Restoration Ecology*, **20**, 65–75.

Neckles, H.A., Dionne, M., Burdick, D.M., Roman, C.T., Buchsbaum, R. & Hutchins, E. (2002) A monitoring protocol to assess tidal restoration of salt marshes on local and regional scales. *Restoration Ecology*, **10**, 556–563.

Onaindia, M., Albizu, I. & Amezaga, I. (2001) Effect of time on the natural regeneration of salt marsh. *Applied Vegetation Science*, **4**, 247–256.

Paramor, O.A.L. & Hughes, R.G. (2005) Effects of the invertebrate infauna on early saltmarsh plant colonisation of managed realignment areas in south-east England. *Marine Ecology Progress Series*, **303**, 61–71.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Race, M.S. & Fonseca, M.S. (1996) Fixing compensatory mitigation: what will it take? *Ecological Applications*, **6**, 94–101.

Ruiz-Jaen, M.C. & Aide, T.M. (2005) Restoration success: how is it being measured? *Restoration Ecology*, **13**, 569–577.

SER (2004) *The SER International Primer on Ecological Restoration*. Society for Ecological Restoration International Science & Policy Working Group. www.ser.org & Tucson: Society for Ecological Restoration International.

Shepard, C.C., Crain, C.M. & Beck, M.W. (2011) The protective role of coastal marshes: a systematic review and meta-analysis. *PLoS ONE*, **6**, e27374. doi:10.1371/journal.pone.0027374.

Short, F.T., Burdick, D.M., Short, C.A., Davis, R.C. & Morgan, P.A. (2000) Developing success criteria for restored eelgrass, salt marsh and mud flat habitats. *Ecological Engineering*, **15**, 239–252.

Simenstad, C.A. & Thom, R.M. (1996) Functional equivalency trajectories of the restored Gog-Le-Hi-Te estuarine wetland. *Ecological Applications*, **6**, 38–56.

Spencer, K.L., Cundy, A.B., Davies-Hearn, S., Hughes, R., Turner, S. & MacLeod, C.L. (2008) Physiochemical changes in sediments at Orplands Farm, Essex, UK following 8 years of managed realignment. *Estuarine Coastal and Shelf Science*, **76**, 608–619.

Stace, C.A. (2010) *New Flora of the British Isles*, 3rd edn. Cambridge University Press, Cambridge, UK.

Stagg, C.L. & Mendelssohn, I.A. (2010) Restoring ecological function to a submerged salt marsh. *Restoration Ecology*, **18**, 10–17.

Sullivan, G., Callaway, J.C. & Zedler, J.B. (2007) Plant assemblage composition explains and predicts how biodiversity affects salt marsh functioning. *Ecological Monographs*, **77**, 569–590.

Turner, R.E., Redmond, A.M. & Zedler, J.B. (2001) Count it by acre of function – mitigation adds up to net loss of wetlands. *National Wetlands Newsletter*, **23**, 5–16.

Varty, A.K. & Zedler, J.B. (2008) How waterlogged microsites help an annual plant persist among salt marsh perennials. *Estuaries and Coasts*, **31**, 300–312.

Williams, P.B. & Orr, M.K. (2002) Physical evolution of restored breached levee salt marshes in the San Fransico Bay estuary. *Restoration Ecology*, **10**, 527–542.

Wolters, M., Garbutt, A. & Bakker, J.P. (2005) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249–268.

Zedler, J.B. (1993) Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. *Ecological Applications*, **3**, 123–138.

Zedler, J.B. (2004) Compensating for wetland losses in the United States. *Ibis*, **146**, 92–100.

Zedler, J.B., Callaway, J.C. & Sullivan, G. (2001) Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *BioScience*, **51**, 1005–1017.

Zedler, J.B. & Lindig-Cisneros, R. (2000) Functional equivalency of restored and natural salt marshes. *Concepts and Controversies in Tidal Marsh Ecology*, (ed. M.P. Weinstein & D.A. Kreeger), pp. 565–582. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Details of managed realignment (MR), accidentally realigned (AR) and reference salt marsh sites studied.

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