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RESEARCH ARTICLE

Restored saltmarshes have low beta diversity due to limited topographic variation, but this can be countered by management

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Abstract

1. Spatial heterogeneity of species (beta diversity) is an important attribute of ecological communities, but is less frequently considered when assessing restoration success than other aspects of diversity (gamma and alpha). Differences in beta diversity between restored and natural sites may arise due to differences in environmental heterogeneity.
2. We used a nested sampling design to survey plant communities and environmental conditions (elevation, redox potential and metrics of topography) on four pairs of restored and natural saltmarshes. We assessed whether there were differences in both alpha and beta diversity between natural and restored sites and analysed their environmental drivers.
3. Topography was an important driver of plant alpha diversity and beta diversity on saltmarshes. The effects of topography were partly indirect, mediated through changes in redox potential, but topography also influenced plant communities independently of both elevation and redox.
4. Restored saltmarshes were less heterogeneous in topography than natural marshes. This reduced topography was reflected in lower beta diversity; plant communities 1 m apart in natural marshes were as dissimilar as those found 20 m apart in restored marshes.
5. Large-scale topographic manipulation carried out at one site a decade after initial restoration successfully increased topographic heterogeneity and increased beta diversity when surveyed 3 years after manipulation. These changes were still evident when resurveyed after a further 2 years.
6. *Synthesis and applications.* Increasing environmental heterogeneity can improve restoration outcomes by increasing beta diversity on restored sites. The effect of environmental heterogeneity is likely to be particularly strong within intertidal habitats such as saltmarshes, where small changes in topography can determine whether a species can occur at a given location. Topographic manipulation is a feasible post-restoration technique that can be applied to ensure restored

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saltmarshes better meet policy targets of biological, physical and functional equivalence with natural marshes.

KEYWORDS

habitat creation, heterogeneity, managed realignment, management intervention, plant community, saltmarsh, tidal marsh, topography

1 | INTRODUCTION

Ecological restoration is an important strategy to compensate for losses due anthropogenic activity and environmental change (Young, 2000). Successful ecological restoration is embedded in policy targets requiring 'no net loss', 'biological equivalence' or 'net gain' of habitat (Brady & Boda, 2017; McKenney & Kiesecker, 2010). Studies evaluating whether restoration schemes have succeeded in recreating the physical and ecological conditions found in natural systems have played a valuable role in efforts to understand and predict restoration outcomes (Brudvig, 2017; Wortley et al., 2013). Species diversity is frequently evaluated as a metric of restoration success (Wortley et al., 2013), but it is often only quantified at a site scale (gamma diversity) or sampling point level (alpha diversity). However, spatial variation of diversity within restoration sites (beta diversity) is also an important component of restoration success, but the extent to which beta diversity replicates natural sites is less well-understood (Grman et al., 2013; Martin et al., 2005). Besides having intrinsic value as an aspect of biodiversity, restoring beta diversity is important as higher beta diversity has been linked to greater simultaneous provision of a range of ecosystem services (Grman et al., 2018).

Where beta diversity has been found to differ between restored and natural sites, it is thought that differences may relate to environmental heterogeneity (e.g. local variation in soil properties or elevation) and its effect on what species can occur in a given location (Larkin et al., 2016), or from dispersal limitation restricting the pool of species that can colonise a restored site (Grman et al., 2015; Vellend et al., 2007). Elucidating the cause of differences in beta diversity between natural and restored sites has implications for restoration management. If differences are primarily due to dispersal limitation, then they are likely to reduce over time as restored sites develop (Grman et al., 2013). However, if differences result from environmental heterogeneity, management interventions to alter the physical environment are likely to be needed.

The nature of environmental heterogeneity varies from subtle changes in environmental conditions modifying the favourability of a location for a species to more marked environmental variation that constrains whether a species can occur in a location at all. An example of subtle changes in favourability is variation in nutrient levels on land previously used for agriculture; in these systems, variation in beta diversity does not appear driven by environmental heterogeneity (Baer et al., 2016; Grman et al., 2015; Grman & Brudvig, 2014).

However, environmental heterogeneity is likely to be more important when variation is large enough to impose stronger environmental filters on species occurrence. Intertidal systems such as rockpools and saltmarshes have strong environmental filtering, with species distributions showing marked zonation along environmental gradients that manifest over one to hundreds of metres (Chapman, 1939; Lawrence, Evans, et al., 2021). However, patterns of beta diversity have not been compared between restored and natural saltmarshes.

Saltmarshes are typically restored through managed realignment (MR), where sea walls are breached to reinstate tidal flow to the land behind. The plant communities that develop on these restored marshes are not equivalent to those found on natural marshes, even after more than 50 years of development, with some species that are abundant on natural marshes being rare or absent from restored marshes (Mossman et al., 2012a). These differences in plant communities can be partly explained by broad differences in elevation and sediment redox potential (Sullivan et al., 2018), which are important drivers of saltmarsh plant occurrence as species differ in their ability to tolerate frequent inundation and associated waterlogged soils (Ewanchuk & Bertness, 2004). Restored saltmarshes tend to be at lower elevations relative to the tides than natural marshes and so experience more frequent inundations (Mossman et al., 2012a). Restored saltmarshes may also have altered soil properties that result in poorer drainage (Masselink et al., 2017; Spencer et al., 2017) and thus lower sediment redox potential (Davy et al., 2011). However, differences in plant communities still remain after controlling for these environmental conditions (Sullivan et al., 2018), indicating that other factors must be involved in causing differences in plant communities between restored saltmarshes and their natural counterparts.

Restored saltmarshes also differ from natural marshes in terms of their environmental heterogeneity, with lower topographic heterogeneity in restored sites (Lawrence et al., 2018). Variation in surface topography (humps and pools) influences water drainage and therefore sediment redox potential (Fivash et al., 2020) and so affects plant colonisation and survival, even after accounting for elevation (Mossman et al., 2020). Topography can also alter seed dispersal and emergence patterns through trapping and retaining more seeds as well as by modifying environmental conditions (Wang et al., 2019; Xie et al., 2019). It is for these reasons topography makes a strong candidate for explaining differences in plant communities, including beta diversity.

We survey four pairs of restored and natural saltmarshes and conduct detailed field measurements of plant communities, local

topography and sediment redox potential. We use our nested sampling design to assess whether differences in environmental heterogeneity between restored and natural marshes are reflected in differences in beta diversity. We also evaluate the success of large-scale topographic manipulation (TM), carried out at one site, in replicating the topography and beta diversity found in natural saltmarshes. We present costs and practical details for this scheme, as these are infrequently reported in the literature and these have been reported as barriers to the implementation of restoration actions (Evans et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study sites

We selected four MR sites along the east coast of the United Kingdom, varying in the number of years since the restoration of tidal inundation from 4–20 years. These were Tollesbury (51.7671 N, 0.8378 E; 19 years since restoration at the time of sampling), Orplands (51.7191 N, 0.8631 E; 20 years), Freiston Shore (52.9623 N, 0.0898 E; 12 years) and Deveraux Farm (51.8564 N, 1.2478 E; 4 years). These MR sites were selected as they had natural saltmarsh immediately outside the MR walls (Table S1). All sites were in the south-east of England and in the same geographic zone of saltmarsh plant communities (Adam, 1978). None of the sites had evidence of current grazing by livestock. Permission to conduct fieldwork was obtained from private and NGO landowners and managers.

In addition, we selected a second area of Freiston Shore MR where TM had been conducted as a management intervention to create greater intertidal habitat diversity within the site, without detriment to its flood defence properties. The manipulations occurred 10–14 years after the reinstatement of tidal flow (RSPB unpublished report 2012, Appendix S1), with the area we surveyed being manipulated 10 years after the initial restoration. To our knowledge, this is the first time that post-breaching modifications of this scale have been conducted on a MR site in order to improve biodiversity outcomes. The TM included the creation of shallow lagoons and scrapes (10–40 cm in depth), with the material excavated from these used to create raised levees, plateaux and hillocks (Figure 1).

2.2 | Field sampling

The paired natural and MR sites were surveyed at the same time. Deveraux Farm, Tollesbury and Freiston Shore were surveyed in July 2015, and Orplands was surveyed in August 2016. The topographically manipulated area of Freiston Shore was surveyed in July 2015 and September 2018, returning to the same locations (within $1.82\text{ m} \pm 0.99\text{ SD}$), resulting in samples 3 and 5 years since the management intervention was carried out.

To quantify spatial heterogeneity in local vegetation composition and environmental conditions, we established a nested sampling

scheme with measuring points at both large spatial resolution over a $50 \times 50\text{ m}$ grid and at finer resolution within subregions of that grid (Figure 1c). Specifically, measuring points were located every 10 m within the $50 \times 50\text{ m}$ grid. Eight of these measuring points were randomly selected (the same locations used in each grid) to establish further clusters of sampling points. In each cluster, sampling points in the four cardinal directions were established at 1 m and 2 m from the central point creating a cross formation with a total of nine sampling points. This nested design resulted in 100 sampling points per grid, with replication across horizontal distances from 1 to 72.5 m. For each study site ($n = 4$), one grid was established in the natural marsh and one in the MR; for Freiston Shore, one grid was also established in the topographically manipulated area. Grids were centred on the middle elevations of the marsh, avoiding artificial features (walls, paths etc.).

At each sampling point ($n = 100$ per grid except Deveraux Farm restored where $n = 94$), data on vegetation, redox potential and elevation (m above UK reference mean sea level) were collected. Vegetation was assessed by recording the percentage cover to the nearest 5% (assessed by eye, assigning rare species a value of 1%) of each vascular plant species in a $0.5 \times 0.5\text{ m}$ quadrat placed at the centre of each sampling point, giving us the list of species occurring in each quadrat and data on their abundance used to calculate diversity metrics. The area (%) of bare (unvegetated) ground in each quadrat was also recorded. Redox potential was measured at the centre of each quadrat with a Campbell Scientific calibrated ORP Probe (-700 to $+1,100\text{ mV}$), at a soil depth of approximately 5 cm, left until the reading stabilised (~ 5 min). Elevation relative to the UK reference mean sea level (Ordnance Datum Newlyn, ODN) was measured at each location using a differential GPS (Trimble R10). Elevation above ODN was converted to the local datum (elevation in tidal frame), where 0 equates to mean high water neap and 1 equates to mean high water spring tide level, to enable comparisons between sites as tidal variation can change dramatically over small geographic distances (Mossman et al., 2012b).

To quantify the local topography at each sampling point, the elevation was measured at 1 m distances (horizontally) from each sampling point in the four cardinal directions. Using these measurements, we derived two topographic indices, namely rugosity and relative topographic position (a form of topographic position index, Gallant, 2000). These indices capture complementary aspects of topography (uncorrelated in our data, Figure S1), with rugosity providing a value of the magnitude of surface variation but not direction, and relative topographic position indicating the direction but not the magnitude of surface variation. Rugosity was calculated as the standard deviation of elevation of the sampling point and its surrounding four points. Relative topographic position was calculated as $P = 2 \times (Z_s - Z_{\min}) / (Z_{\max} - Z_{\min}) - 1$, where P is relative topographic position, Z_s is the elevation of the central sampling point and Z_{\min} and Z_{\max} are the minimum and maximum elevation across the sampling point and its surrounding four points respectively. We chose to compare the central sampling point to the minimum rather than mean elevation of surrounding

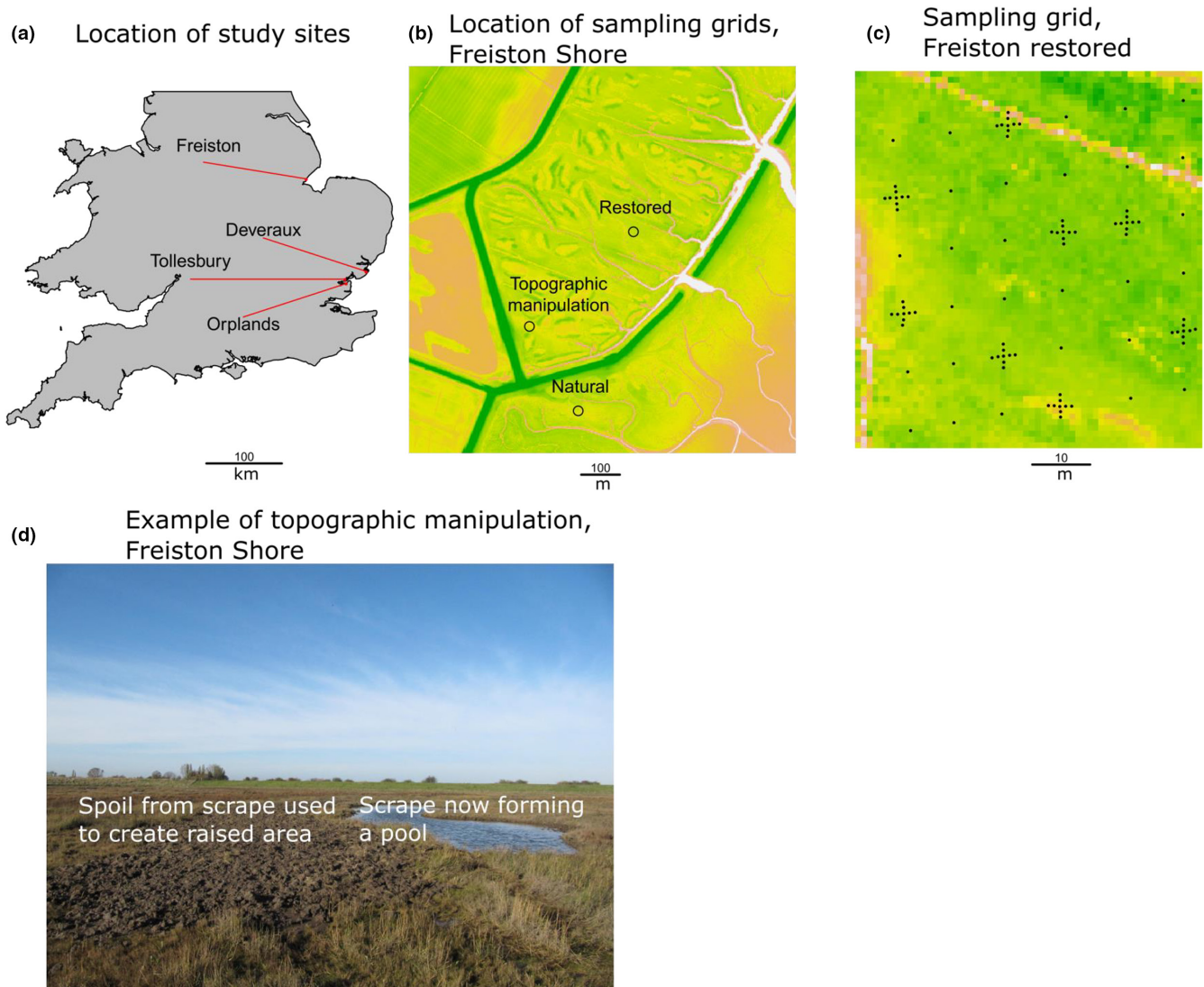


FIGURE 1 Sampling design used in this study. (a) Location of the four study sites. (b) Locations of sampling grids on natural and restored saltmarsh at Freiston Shore (separated by the sea wall, dark green), including an area of topographic manipulation. (c) Example of a sampling grid (the restored marsh at Freiston Shore) with each dot showing the location of a sampling point. (d) Example of the topographic manipulation conducted by the Royal Society for the Protection of Birds. (b) and (c) are plotted on a 1-m resolution digital terrain model derived from LiDAR imagery collected by the Environment Agency (UK Government, 2018). Note that these LiDAR-derived elevations were not used in this paper; all elevation data used were collected with differential GPS

sampling points to capture the full range of variation in the local environment. Relative topographic position index ranges between -1 and 1 ; values of -1 indicate that the central sampling point is the lowest (of the five sampled) and 1 indicates it is the highest sampling point.

2.3 | Calculation of diversity

For each quadrat, we calculated species richness from the list of species in each quadrat and Shannon diversity (Hill, 1973) using the percentage cover to indicate abundance using the diversity function in the `VEGAN` R package (Oksanen et al., 2020). These calculations give the two metrics of quadrat-scale alpha diversity.

We used two approaches to calculate beta diversity, firstly as an additive partition of alpha and gamma diversity (Veech et al., 2002) and secondly as the dissimilarity of pairs of sampling points (Burnham, 2004). For clarity, we refer to these as partitioned beta diversity and dissimilarity beta diversity. Partitioned beta diversity was calculated at two spatial scales: cluster level (eight clusters of nine plots within 4 m of each other per sampling grid, i.e. crosses in Figure 1c) and sampling grid level. Cluster-level partitioned beta diversity was calculated by subtracting quadrat-level alpha diversity from cluster-level gamma diversity (the latter being the total number of species found in the sampling cluster), while grid-level partitioned beta diversity was calculated by subtracting the number of species in each cluster from the total number of species found in a sampling grid (grid-level gamma diversity). Dissimilarity beta diversity

quantified the dissimilarity of plant community composition between pairs of quadrat-level sampling points. Community dissimilarity was calculated using Jaccard's index (`vegdist` function in the `VEGAN` R package, Oksanen et al., 2020), treating bare ground as a species because (a) the measure cannot be calculated where no species are present and (b) we consider the absence of plants to be ecologically relevant. Our results are not driven by the inclusion of bare ground as we obtained similar inferences using partitioned beta diversity where bare ground was not included.

2.4 | Data analysis

Analyses were conducted in R version 4.02 (R Core Team, 2021). To examine the drivers of richness and diversity, we fitted linear models with either redox potential, elevation in tidal frame or topography (rugosity, relative topographic position and their interaction) as explanatory variables. This was done separately for natural and restored marshes. We included site as a fixed effect in all models to account for large-scale variation between the four areas as well as differences in age between the sites; the decision to treat site as a fixed rather than random effect was based pragmatically on the low number of factor levels. We fitted all combinations of these variable sets (i.e. redox + topography metrics, redox + elevation in tidal frame etc.), including a site-only null model, and used hierarchical partitioning (the `'partition'` function in the `HIER.PART` R package, Walsh & Mac Nally, 2013) to determine the proportion of variation explained by each variable set. We examined the environmental controls on plant community composition using multivariate binomial GLMs implemented in the `MVABUND` R package (Wang et al., 2012). While in natural marshes explanatory variables were not strongly correlated with each other ($|r| < 0.5$), in restored marshes elevation in the tidal frame was strongly positively correlated with redox potential ($r = 0.801$, Figure S1). Despite this, variance inflation factors were relatively low (≤ 2.36 for the natural marsh model and ≤ 4.04 for the restored marsh model).

To examine how redox potential related to the topography metrics and elevation in tidal frame, we fitted linear models with elevation in tidal frame, topography variables (rugosity, relative topographic position and their interaction) or both elevation in tidal frame and topography as explanatory variables (including site in all models) and used hierarchical partitioning as above to determine the proportion of variation explained by each variable set in restored and natural marshes.

We used linear and Poisson GLMs with marsh restoration status (restored or natural) as an explanatory variable to test if species richness, Shannon diversity and the environmental variables differed with restoration status. These models had restoration status and site as explanatory variables. We then examined if differences in plant species richness and diversity were sensitive to large-scale environmental differences between restored and natural marshes by adding elevation in the tidal frame and redox potential as explanatory variables. We repeated this procedure for partitioned beta diversity and

gamma diversity at sampling cluster level. Statistical analysis could not be conducted on grid-level beta and gamma diversity due to the small sample size at this scale.

To assess the distance decay in the similarity of plant species composition (dissimilarity beta diversity) and environmental variables between sampling points, we fitted local polynomial regression (LOESS) models of dissimilarity against pairwise horizontal distance between sampling points. These were conducted separately for each sampling grid, and uncertainty around model fits was assessed by randomly resampling data with replacement 1,000 times and refitting LOESS models to the resampled data to calculate the mean and upper/lower 95% confidence intervals of the LOESS fits. This analysis was conducted for plant community dissimilarity (Jaccard's index) and for differences in elevation and redox potential. Correlations between dissimilarity matrices were tested using Mantel tests, with 1,000 permutations.

3 | RESULTS

3.1 | Drivers of alpha diversity in restored and natural saltmarshes

On natural saltmarshes, topography metrics (rugosity, relative topographic position and their interaction) were an important driver of plant species richness, Shannon diversity and composition, independently explaining 42.9% of explained variation in species richness and 39.4% of variation in Shannon diversity (Table 1). There was a statistically significant interaction between rugosity and relative topographic position, meaning that the effect of rugosity on richness and diversity switched from being negative at low relative topographic position to positive at high relative topographic position (Table 1). This indicates that plant species richness and Shannon diversity were lower in depressions and higher on raised features such as hillocks. These direct effects of topography were likely enhanced by indirect effects through altered sediment redox potential, as 49.4% of explained variation in redox potential in natural marshes was also due to the topography metrics. Plant species richness and diversity increased with redox potential (Table 1), and redox potential was lower in depressions and higher in raised features (indicated by the interaction between rugosity and relative topographic position in the model of redox, Table S3).

On average, rugosity was lower in restored marshes (Figure S1), and here the topographic metrics were less important as a driver of plant species richness, diversity and composition (e.g. independent effect of topography metrics on species richness = 13.3% on restored marshes, Table 1) or of redox potential (Table S3, Figure S1). Plant species richness was lower in restored than in natural marshes (Poisson GLM also accounting for site, difference = -0.19 , $z = 4.9$, $p < 0.001$, Figure 2), but this difference was no longer statistically significant when redox potential and elevation in the tidal frame, which were both significantly lower in restored marshes (Figure S2), were included in the model (difference in species richness = -0.05 ,

TABLE 1 Environmental correlates of plant species richness, diversity and community composition. For richness and diversity, coefficients and their standard errors from linear models as well as results of hierarchical partitioning to determine the independent effects of the elevation in tidal frame, redox potential and topography variable sets are shown. For species coefficients, *F* values for each term from multivariate linear models of species composition as a function of environmental variables are shown. Models were fitted separately for restored and natural marshes. Site was included as a fixed effect in all models. Statistical significance codes are *** $p < 0.001$, ** $p < 0.01$ and * $p < 0.05$

Variable	Species richness				Shannon diversity				Species composition			
	Natural		Restored		Natural		Restored		Natural		Restored	
	Coefficient	Variation explained (%)	Coefficient	Variation explained (%)	Coefficient	Variation explained (%)	Coefficient	Variation explained (%)	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
Elevation in tidal frame	0.479 ± 0.173**	41.4	0.154 ± 0.255	27.7	0.475 ± 0.115***	43.3	-0.278 ± 0.177	17.2	111.8***	426.2***		
Redox potential	0.001 ± <0.001	15.7	0.002 ± <0.001***	59.0	0.001 ± <0.001*	17.3	0.002 ± <0.001***	53.9	76.7***	273.9***		
Topography												
Rugosity	-1.484 ± 0.487**	42.9	-4.386 ± 1.640*	13.3	-0.983 ± 0.293***	39.4	-4.905 ± 1.025***	29.0	63.3**	38.2*		
Relative topographic position	-0.035 ± 0.047		-0.001 ± 0.055		-0.039 ± 0.037		0.051 ± 0.0407		17.1	15.4		
Rugosity: Relative topographic position	1.456 ± 0.541**		2.942 ± 2.031		0.880 ± 0.332**		1.192 ± 1.255		55.6**	6.7		

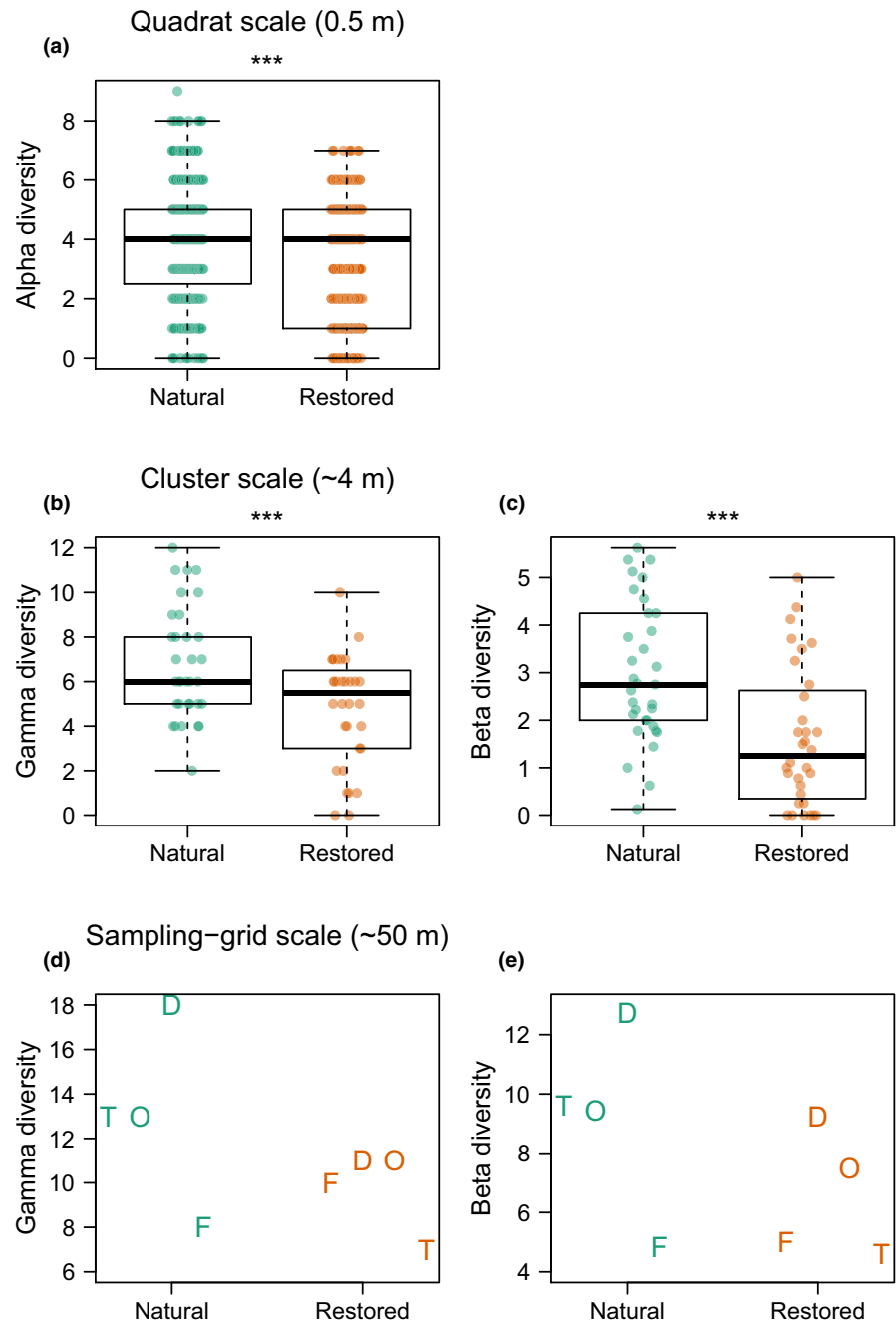
$z = 1.4, p = 0.162$). Similarly, plant Shannon diversity was lower in restored than in natural marshes (difference = $-0.22, t = 5.6, p < 0.001$, Figure S2), but this effect weakened when redox and elevation in the tidal frame were included in the model (difference = $-0.08, t = 2.4, p = 0.017$). Thus, while the topography metrics were an important driver of plant species richness and diversity in natural marshes, differences in alpha diversity between restored and natural marshes were largely explained by differences in elevation and redox.

3.2 | Beta diversity in restored saltmarshes

Partitioned beta diversity, calculated at sampling cluster-scale (~4 m), was lower in restored than in natural marshes (linear model accounting for site, difference = $-1.38, t = -4.3, p < 0.001$, Figure 2) and this was robust to accounting for average cluster-level elevation and redox potential (difference between restored and natural sites = $-1.05, t = -3.5, p = 0.001$). However, the difference in partitioned beta diversity between restored and natural marshes was no longer statistically significant once rugosity was included in the model (difference = $-0.50, t = -1.3, p = 0.184$), indicating that rugosity (which was positively related to beta diversity, slope = 7.0, $t = 2.4, p = 0.018$) partially accounted for the difference in beta diversity between restored and natural saltmarshes. At sampling grid scale (~50 m), partitioned beta diversity and gamma diversity were also lower in restored than in natural marshes (Figure 2), although the small sample size (four sites) precluded formal statistical analysis.

The conclusion that beta diversity is lower in restored saltmarshes, and that this is linked to lower topography, is supported by an alternative analysis looking at the distance decay in the similarity of plant species composition (dissimilarity beta diversity) and environmental conditions. Neighbouring sampling points were, on average, more dissimilar in their elevation, redox potential and species composition in natural marshes than in restored marshes (Figure 3), indicating greater local-scale beta diversity and environmental heterogeneity. Dissimilarity in the environmental conditions and plant species composition increased with distance between the sampling points, but this increase in dissimilarity was less marked in natural marshes than in restored marshes (Figure 3), supported by weaker Mantel correlations between distance and elevation, redox and plant community dissimilarity in natural marshes (Table S4). Although natural marshes had more variation in elevation at finer scales, this difference between restored and natural marshes was reduced or eliminated at larger scales (Figure 3). Differences in redox potential were on average greater in restored marshes for points over 15 m apart, while vegetation dissimilarity was only similar in restored and natural marshes for points over 20 m apart (Figure 3). In both natural and restored marshes, differences in redox potential were positively correlated with differences in elevation (Mantel tests, $r \geq 0.31, p \leq 0.005$, Table S5). Likewise, differences in plant community composition were positively correlated with differences in elevation (Mantel tests, $r \geq 0.31, p \leq 0.001$, Table S5) and differences in redox (Mantel

FIGURE 2 Difference in alpha, beta and gamma diversity between natural and restored saltmarshes. (a) Species richness (alpha diversity) of sampling points, (b, c) gamma and partitioned beta diversity of the nested clusters of sampling points within sampling grids (d, e) gamma and partitioned beta diversity of sampling grids. Statistical significance codes for differences between natural and restored marshes are *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS $p \geq 0.05$



tests, $r \geq 0.20$, $p \leq 0.001$, Table S5). This indicates that differences in elevation between sampling points (i.e. topography) are reflected in differences in redox potential and plant community composition (as measured by dissimilarity beta diversity).

3.3 | Effect of management intervention (experimental topographic manipulation)

Topographic manipulation at Freiston Shore (conducted for site management) increased topographic heterogeneity over small distances, indicated by higher rugosity in the manipulated region than in the unmanipulated MR in both time points (Table S6). In contrast, plant

species richness and diversity were lower than in the unmanipulated restored marsh (Table S6). Topographic manipulation also increased larger scale topographic heterogeneity, with differences in elevation between sampling points equivalent to, or greater than, that seen on natural marshes, particularly when sampling points were at least 5 m apart (Figure 4). This increased topographic heterogeneity was evident in both the sampling periods (T1 and T2) and was reflected by greater variation in redox potential and greater dissimilarity beta diversity (Figure 4). Similarly, the analysis of cluster-scale partitioned beta diversity also supported the recovery of beta diversity in the TM treatment, with no significant difference in beta diversity from the natural marsh in either time point (T1, difference = -0.25 , $t = 0.4$, $p = 0.673$; T2, difference = -0.28 , $t = 0.5$, $p = 0.635$).

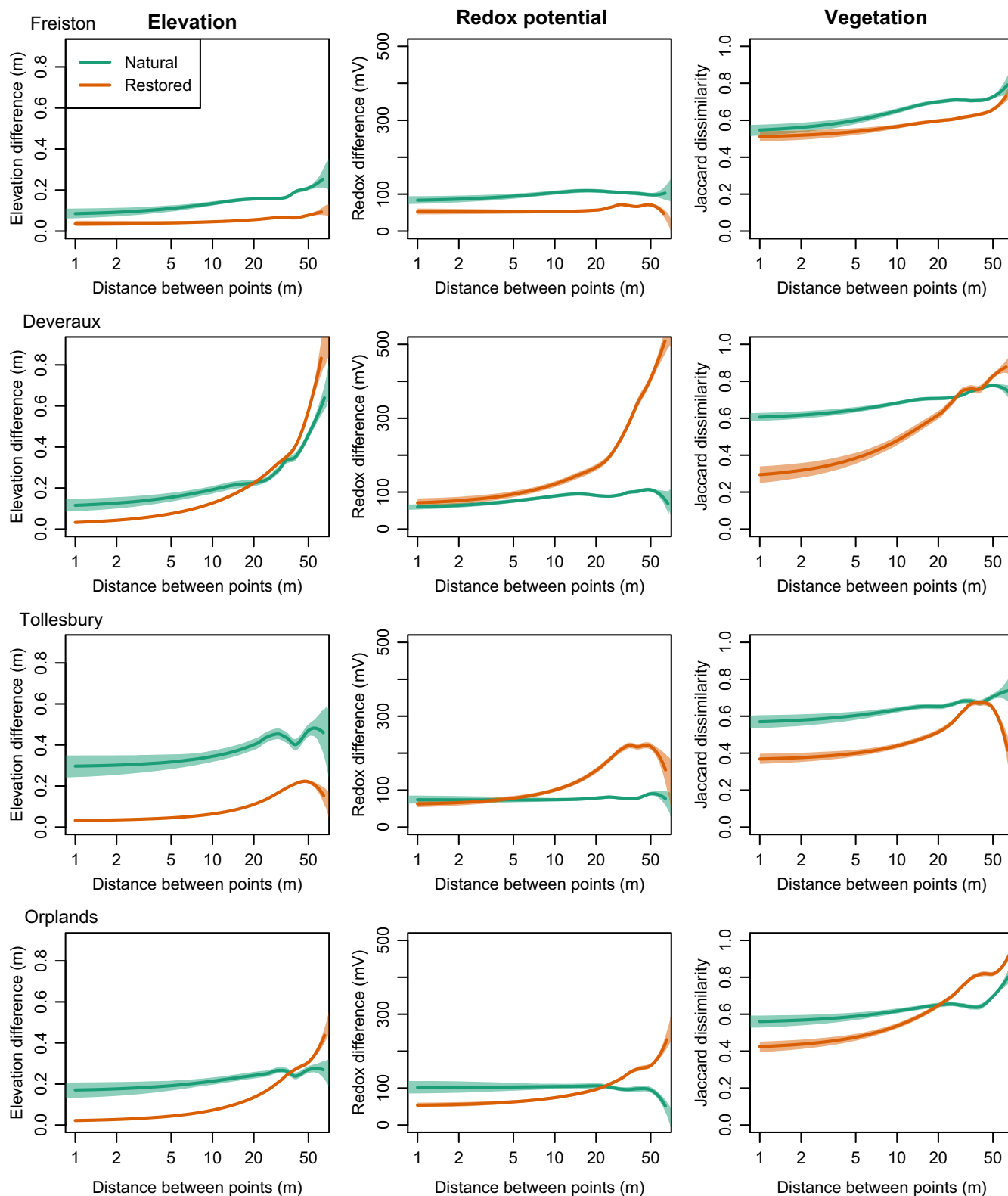


FIGURE 3 Change in difference between pairs of sampling points in terms of elevation, redox potential and plant community composition with distance between points in restored and natural marshes at each site. Locally weighted polynomial (LOESS) models were fitted for each sampling grid, with 95% confidence intervals around each fit assessed by randomly resampling the data with replacement and refitting LOESS models 1,000 times. Underlying data are shown in Figure S3

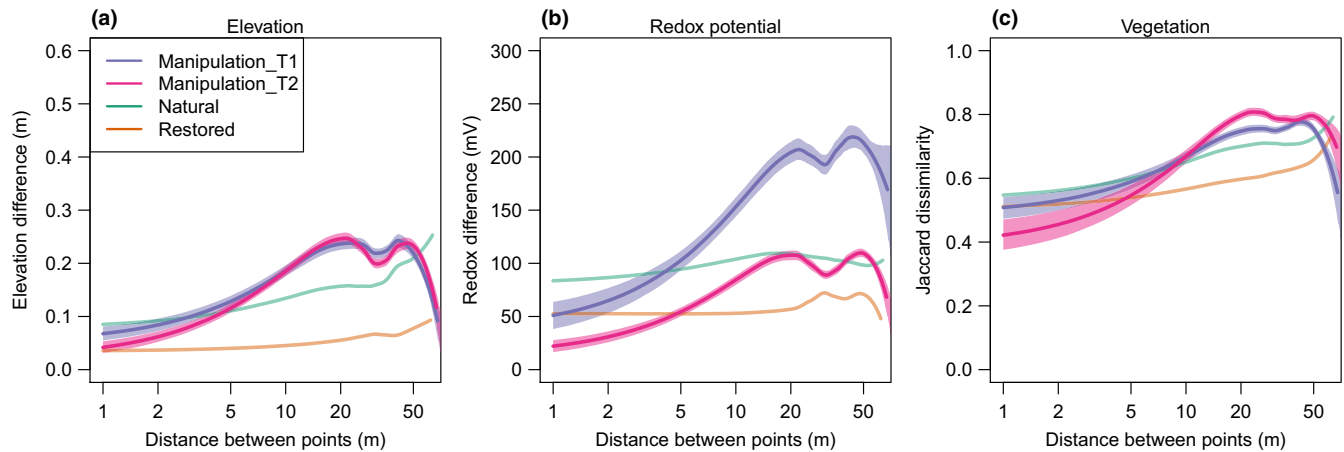


FIGURE 4 Change in difference between pairs of sampling points in terms of (a) elevation, (b) redox potential and (c) plant community composition with distance between points. LOESS fits and bootstrapped 95% confidence intervals are shown for the topographic manipulation area at Freiston Shore in both the sampling periods. Relationships from the natural and restored marsh at Freiston Shore are also shown. Underlying data are shown in Figure S4

4 | DISCUSSION

We find that the beta diversity of plant communities is lower in restored saltmarshes than in natural ones; partitioned beta diversity is lower in restored marshes at both cluster and sampling grid scales, while the lower dissimilarity beta diversity means that on average one would have to walk ~20m across a restored saltmarsh to encounter plant communities as dissimilar as can be found 1 m apart in natural saltmarshes. This lower beta diversity is related to the lower topographic heterogeneity of restored saltmarshes as (a) both local-scale variation in elevation around sampling points (rugosity) and differences in elevation between nearby sampling points were lower in restored marshes than in natural marshes; (b) sampling points that were more similar in their elevation had more similar sediment redox potentials; (c) differences in plant community composition between sampling points (dissimilarity beta diversity) increased with differences in elevation and redox; (d) partitioned beta diversity was lower in restored marshes, even when accounting for restored sites tending to be lower in the tidal frame and having lower redox potential, but this difference was explained by accounting for topography; and (e) habitat management to increase topographic heterogeneity restored both partition and dissimilarity beta diversity to levels similar to that found in natural marshes. This indicates that the lack of topographic heterogeneity and associated low beta diversity on restored marshes can be rectified by management action.

We also found that fine-scale topography (~1-m scale variation around sampling points) influenced alpha diversity and plant species composition, both by changing surface elevation and sediment redox potential and by having an effect independent of these variables. However, while alpha diversity was lower in restored than in natural marshes, this was primarily due to the lower elevation and redox potential of these sites rather than their lower topographic heterogeneity.

4.1 | Effect of topographic heterogeneity on plant communities

We found that restored saltmarshes had reduced surface topography compared to natural marshes. In the immediate vicinity of sampling points, there was less variation in elevation in restored marshes (i.e. lower rugosity) but the form of topography (concave vs convex features, indicated by relative topographic position) did not differ, while at coarser scales, differences in elevation between pairs of sampling points up to 50m apart were typically lower in restored marshes. This supports results from another field study at one site (Brooks et al., 2015) and from a multi-site analysis of remote sensing data (Lawrence et al., 2018). The lower topographic heterogeneity in restored saltmarshes might explain why restored saltmarshes fail to develop biologically equivalent plant communities to natural marshes (Mossman et al., 2012a). We show that local (~1 m scale) topographic variation can affect plant communities by changing the elevation and redox conditions, which are both known to be important determinants of plant distribution within saltmarshes (Davy et al., 2011). Redox potential increases with height in the tidal frame due to reduced tidal duration, but this relationship is modified by topographic features (Castellanos et al., 1994; Varty & Zedler, 2008). Raised features (e.g. hillocks) have better drainage, so have higher redox potentials than expected for their position in the tidal frame, while poorly drained depressions have low redox for their elevation in the tidal frame (Fivash et al., 2020). The position of topographic features influences their effect, as small-scale experiments indicate that raised topographic features (which increase drainage) have a disproportionately strong effect on sediment redox potential when low in the tidal frame (Cui et al., 2011; Mossman et al., 2020; Varty & Zedler, 2008). The variation in environmental conditions created by topography may promote species coexistence (and therefore higher diversity) by facilitating niche differentiation (Varty & Zedler, 2008); some species such as *Limonium vulgare* are associated with low redox conditions high in

the tidal frame, while higher redox conditions at the same elevation favour species such as *Atriplex portulacoides* (Sullivan et al., 2018), and lowered topographic features (which increase moisture retention and reduce redox potential) at high elevations in the tidal frame are effective at supporting plant species that are typically under-represented on restored saltmarshes (Mossman et al., 2020). Our results show that topography can also affect plant occurrence independently of changes in elevation and redox, supporting the results of a previous small-scale experimental study (Mossman et al., 2020). This could occur through reduced seedling retention and survival in depressions as a result of high levels of sedimentation (Bouma et al., 2016; Wang et al., 2019), accumulation of salts within areas of high evaporation (Hladik & Alber, 2014; Largier et al., 1997) or potentially greater droughting on raised humps (Xie et al., 2019). Our results support the operation of these direct effects of topography alongside those indirect effects via redox potential (Table S3). The importance of direct effects of topography in influencing vegetation development is highlighted prominently as in natural marshes topography exerted an independent effect on plant species richness, diversity and community composition of similar magnitude to that of elevation and redox (Table 1).

Our results suggest that lack of topographic heterogeneity in restored saltmarshes leads to more homogenous plant communities (i.e. lower beta diversity), as the lower difference in elevation between sampling points in restored marshes is reflected in lower dissimilarity in plant communities. An alternative explanation for the lower beta diversity in restored saltmarshes is that it is a legacy of colonisation patterns, with species having more clumped distributions as vegetation patches expand following initial colonisation (Martin et al., 2005). However, this explanation is unlikely as two lines of evidence support the role of topography as a driver. Firstly, differences in plant community composition are greatest when differences in elevation are greatest, and this correlation is stronger than that with distance. Secondly, experimental TM increased vegetation heterogeneity, when this action would be expected to decrease heterogeneity if it was due to colonisation dynamics as the disturbance would have reset the plant community to an earlier phase of colonisation (Martin et al., 2005). Although colonisation dynamics are unlikely to explain the more homogenous plant communities in restored saltmarshes, they could interact with topographic heterogeneity to shape diversity patterns. A greater environmental heterogeneity in natural marshes could enhance species coexistence through spatial niche partitioning (Chesson, 2000), where variation in the environment tips the balance of competitive interactions in favour of certain species differentially over space (Amarasekare, 2003). Although we did not test whether the differences in environmental conditions were sufficient to alter competitive interactions, it is likely that they would be, given the relatively subtle variation in the niches of different saltmarsh plant species (Bertness, 1991; Sullivan et al., 2018). The potential for environmental heterogeneity to enhance the local-scale coexistence of species may be especially high in saltmarshes as several dominant species (e.g. *Atriplex portulacoides*, *Puccinellia maritima* and *Spartina anglica*)

spread by vegetative growth (Chapman, 1950). The expansion of clones of these species is likely to be limited in natural marshes by encountering patches of unsuitable environmental conditions, whereas the more homogenous environment in restored marshes is likely to allow them to expand more widely as their niches are continuously connected on a flat surface.

4.2 | Creating topographic heterogeneity on restored sites

We evaluated the success of a post-restoration TM scheme, instigated 10 years after restoration. We found that this successfully and persistently enhanced topographic heterogeneity. This was particularly pronounced when comparing sampling points at least 5 m apart, but we also found that fine-scale topographic heterogeneity, measured as the rugosity at each sampling point, increased following TM. The latter was finer scale than the deliberately created topographic features, so is likely to have resulted from disturbance during construction (e.g. tyre tracks).

The success of this post-restoration TM at enhancing environmental heterogeneity and plant beta diversity demonstrates the potential for management actions at other restored saltmarshes. These post-restoration manipulations were relatively inexpensive (£20k for work over 66 ha at Freiston Shore, compared to initial costs of site creation of £600k, John Badley, RSPB pers. comm.), so could feasibly be expanded to some of the 99 existing intertidal schemes in Europe (APBmer Online Marine Registry, 2020). For future MR sites, it will be cheaper to increase topography prior to reinstating tidal flow, as machinery is already on site. However, these features may be lost due to the rapid sedimentation that typically follows the reinstatement of tidal flow (Elschot & Bakker, 2016; Spencer et al., 2012), meaning that post-restoration manipulation carried out after this initial sedimentation is more likely to persist. A further potential benefit of post-restoration manipulation is that it may break up hard layers of sediment (aquiclude) that often develop on restored saltmarshes (Spencer et al., 2017).

Besides restoring plant community heterogeneity, TM is also likely to benefit other taxonomic groups; fish use is related to topographic features in restored saltmarshes (Larkin et al., 2008), while hillocks provide unflooded areas for nesting and roosting birds (Dias et al., 2006). Indeed, the density of breeding common redshank *Tringa tetanus* at Freiston Shore increased following TM (Ausden et al., 2019). We recommend monitoring the success of future TM schemes to increase the confidence with which the effect of restoration can be separated from idiosyncratic succession (Stuble et al., 2017), which is currently limited by the lack of replication.

AUTHORS' CONTRIBUTIONS

P.J.L. and H.L.M. designed the sampling methodology and collected the data; P.J.L. and M.J.P.S. analysed the data. All authors wrote and approved the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.8w9ghx3np> (Lawrence, Sullivan, et al., 2021).

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