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What factors determined restoration success of a salt marsh ten years after de-embankment?

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Keywords
Artificial salt marsh; Elevation; Grazing; Halophytes; Long-term study; Managed realignment; Salinity; Soil drainage; Soil redox

Abbreviations
MHT = mean high tide; NFB = Noard-Fryslân Bûtendyks.

Nomenclature
van der Meijden (2005)

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Abstract

Questions: How successful was the restoration of a salt marsh at a former summer polder on the mainland coast of the Dutch Wadden Sea 10 yr after de-embankment? What were the most important factors determining the level of restoration success?

Location: Noard-Fryslân Bûtendyks, northwest Netherlands.

Methods: The frequencies of target plant species were recorded before de-embankment and monitored thereafter (1, 2, 3, 4, 6 and 10 yr later) using permanent transects. Vegetation change was monitored using repeated mapping 14 yr before and 1, 7 and 10 yr after de-embankment. A large-scale factorial experiment with 72 sampling plots was set up to determine the effects of distance to a breach point, distance to a creek and grazing treatment on species composition. Abiotic data were also collected from the permanent transects and sampling plots on elevation, soil salinity and redox potential.

Results: Ten years after de-embankment, permanent transect data showed that 78% to 96% of the target species were found at the restoration site. Vegetation mapping, however, showed that the diversity of salt marsh communities was low, with 50% of the site covered by the secondary pioneer marsh community. A multivariate analogue of ANOVA indicated that the most important experimental factor determining species composition was the interaction between distance to the nearest creek and livestock grazing. The combination of proximity to a creek and exclusion from livestock grazing always resulted in development of the high marsh community. In contrast, the combination of being located far from a creek, grazed and situated at low elevation with accompanying high salinity resulted in development of the secondary pioneer marsh community.

Conclusions: Using target species as criteria, restoration success could be claimed 10 yr after de-embankment. However, the diversity of communities in the salt marsh was lower than desired. Variable grazing regimes should be applied to high-elevation areas to prevent dominance by single species of tall grasses and to promote formation of vegetation mosaics. Low-elevation areas need lower grazing pressure. Also, an adequate soil drainage network should be preserved or constructed in low-elevation areas before de-embankment.

Introduction

Coastal salt marshes are transitional ecosystems between land and sea, with characteristic assemblages of plants and animals, many of which are restricted to this specific habitat (Heydemann 1981; van der Maarel & van der Maarel-Versluys 1996). Situated as they are in this boundary zone, salt marshes provide valuable ecosystem and societal functions such as providing habitat for breeding waders and migratory waterfowl (Meltofte et al. 1994; Madsen et al. 1999), and cost-effective measures for coastal protection through attenuation of wave energy (Gedan et al. 2011; Möller et al. 2014). Approximately 50% of salt marshes worldwide, however, have been lost or degraded due to processes such as erosion, coastal development and land reclamation (Adam 2002). As a counter measure to this loss and in recognition of the nature conservation value of salt marshes, increasing numbers of salt marshes are being

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created or restored worldwide (Zedler 2000; Wolters et al. 2005). De-embankment is one of the approaches used in salt marsh restoration (also known as managed realignment), where tidal influence is restored over formerly reclaimed land by breaching coastal embankments.

The success of de-embankment in restoring different aspects of salt marsh vegetation has been reviewed for Northwest Europe (Wolters et al. 2005; Garbutt & Wolters 2008; Mossman et al. 2012). For most de-embanked sites, however, only observational data have been collected to monitor changes in vegetation and environmental variables over time, and the whole site is generally treated as a single unreplicated experiment. Studies that experimentally test the factors determining restoration success at a site are less common, and these have concentrated on the dispersal and establishment phases important for short-term success (Lindig-Cisneros & Zedler 2002; Garbutt et al. 2006), the effect of genetic diversity on the structure of ecosystem engineers such as *Spartina alterniflora* (Proffitt et al. 2003), and the effects of N addition (Boyer & Zedler 1999). To accurately predict trajectories of restoration sites after de-embankment, more experiments conducted over a longer time scale are needed.

In order to evaluate the success of a restoration effort, the criteria for success must first be set. Setting criteria using a combination of compositional, structural and functional measures has been recommended (Hobbs & Norton 1996). As a first step for evaluating the success in restoration of salt marsh vegetation at a site, Wolters et al. (2005) proposed a saturation index for the regional target species pool, which is a type of compositional measure. This saturation index, however, should be complemented by more detailed measures of vegetation composition and structure when possible because de-embanked sites have been shown to differ from reference sites in terms of community composition and structure even when salt marsh species were able to rapidly colonize sites after resumption of tidal inundation (Garbutt & Wolters 2008; Mossman et al. 2012). Many aspects of the relationship between biodiversity, which can include both compositional and structural measures, and ecosystem function are still debated. It is likely, however, that different functions require different structural components; thus, high structural diversity is more likely to support higher functionality (Wolters et al. 2005).

Once the criteria for success are set, a factorial experiment combining the factors likely to influence restoration success would allow for assessment of the unique contributions of each factor and identification of interaction effects between factors. In any restoration project, the potential for dispersal and establishment of target species must be considered. In salt marsh restoration projects involving de-embankment, rates of sedimentation are also an important issue because embankment accompanied by drainage for agricultural purposes can lead to lower elevation levels with respect to MHT (mean high tide) in reclaimed land compared to adjacent salt marshes (Bakker et al. 2002). The factor, distance to a breach point, incorporates both dispersal and sedimentation processes over space because the opening in the embankment is the point at which tidal water enters the system, transporting both diaspores and sediment. Thus, areas further from the breach points may receive fewer diaspores and have lower rates of sedimentation than those near breach points, which in turn would affect species composition. How tidal waters leave the system is also an important issue in salt marshes because the zonation of halophytes is partly determined by tolerance to waterlogging (Davy et al. 2011). Sites targeted for de-embankment tend to be relatively flat due to their reclamation history so that artificial creeks may have to be excavated to improve both drainage and colonization rates (Eertman et al. 2002). Additionally, levees may develop along creeks further enhancing soil aeration locally and topographic heterogeneity at larger scales. Thus, areas far from creeks may support species with higher tolerance for waterlogging than those near creeks. Livestock grazing has been shown to be an important factor in both natural and artificial salt marshes (Bakker et al. 2002). In addition to removing biomass, trampling by livestock on clay soils results in soil compaction, which increases saturation of water in the soil, decreases soil redox potentials, and reduces decomposition activity (Schrama et al. 2013). Without livestock grazing, successional trajectories tend towards species-poor communities dominated by *Atriplex portulacoides* at lower elevations and *Elytrigia atherica* at higher elevations. Thus, ungrazed areas are predicted to support competitive species with higher biomass, whereas grazed areas should support species with higher tolerance for trampling effects such as soil compaction and lower soil redox potentials.

These three factors (distance to breach, distance to creek and grazing) are linked in salt marshes to many important abiotic variables associated with elevation level. Elevation within tidal frame is considered the primary determinant of the abiotic factors that drive salt marsh zonation. This variable is correlated with frequency and duration of tidal inundation, rates of sedimentation, salinity and redox potential, but the relationships are not always straightforward (Davy et al. 2011). Appropriate elevation within the tidal frame is a crucial factor in determining the success of salt marsh restoration at a site (Bakker et al. 2002; Wolters et al. 2005). Salinization of the soil is another crucial factor because it is one of the defining characteristics of a salt marsh. From a management perspective, the development of marsh surface elevation and salinity at a restoration site should be explicitly addressed with respect to management options such as those regarding soil drainage and grazing.

The main objectives of this study were: (1) to evaluate the level of success in salt marsh restoration in a former summer polder 10 yr after de-embankment; and (2) to identify the main factors that determined the level of success. The level of success in restoring characteristic salt marsh structure was addressed using two different measures. At the species scale, the presence of salt marsh target species was monitored over time, and success was defined by the saturation level of the target species list. At the community scale, the development of characteristic salt marsh communities was monitored over time, and success was defined by the diversity of the developing salt marsh communities. With respect to the second aim, a large-scale experiment was set up to test the effects of multiple factors on plant species composition; the factors considered were distance to a breach point in the summer dike, distance to a creek, livestock grazing, marsh surface elevation and salinity.

Methods

Site description

The de-embankment site is located at Noard-Fryslân Bûtendyks (NFB), the Netherlands (53°20′ N, 5°45′ E). This site encompasses about 120 ha of land that had been converted from salt marsh into a *summer polder* by embankment in 1909 (Schroor 2009). Although this site is embedded in a larger complex of summer polders on the landward side, there is an adjacent salt marsh that developed outside the summer dike on the seaward side (Fig. 1). Summer dikes are low embankments that are not designed to withstand very high spring tides or storm surges. After conversion, the summer polder was used for summer grazing and, periodically, also for haymaking. Grazing by livestock was continued with cattle and horses after de-embankment. In preparation for de-embankment, three artificial creek systems were excavated for the supply and discharge of seawater and sediment in 2000. In order to rewet the restoration site, the existing grid of ditches (10-m apart) was partly filled in to prevent full drainage into the artificial creeks. The following September in 2001, three breaches of 20–40 m in width were made in the summer dike at the mouths of these artificial creeks to allow for tidal inundation of the study site. Two years following de-embankment, the elevation of the study site varied between 0.30 and 0.90 m +MHT (Mean High Tide; van Duin et al. 2007), but the mean elevation was approximately 20 cm higher in the western than in the eastern part of the site. MHT for the study area was estimated at 1.00 m +NAP (Dutch Ordnance Datum) and tidal amplitude at 2.3 m, based on the gauge stations at Harlingen and Lauwersoog, 30 km west and 30 km east of the study site, respectively. The average annual precipitation was 820 mm (from 1981–2010 at the Leeuwarden Air Base, 12 km south of the study site; data from the Royal Netherlands Meteorological Institute (KNMI)). The soil consists of a clay sediment layer of >1 m in thickness above a sandy sub-layer.

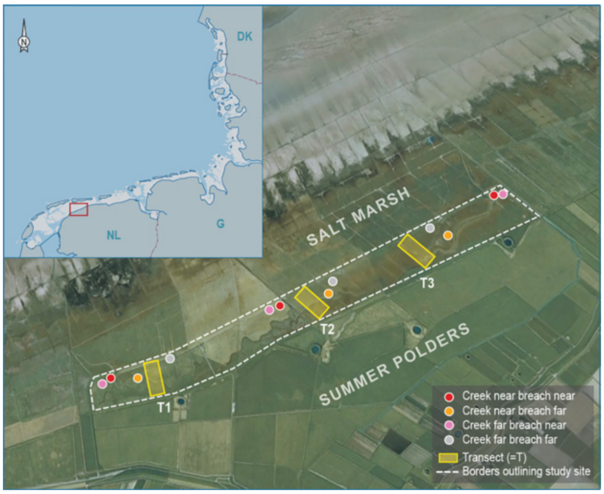

Fig. 1. The site of de-embankment showing locations of the permanent transects and sampling plots representing treatment groups of the experimental design (Google Earth).

Experimental design

An experiment using a randomized block design was set up at the study site in the year before de-embankment in order to test for the effects of various factors on plant species composition (Fig. 1). In each catchment area of the three artificial creeks, four sub-sites were established (spatial blocks): close to the breach and close to the creek, close to the breach and far from the creek, far from the breach and close to the creek, far from the breach and far from the creek. At each of the 12 sub-sites, a livestock exclosure (10 m × 25 m) was established before the start of the first grazing season (spring 2002) after de-embankment with three sampling plots (4 m × 4 m) inside and outside the exclosure. Thus, a total of 72 sampling plots were used to test a full-factorial experiment of distance to breach by distance to creek by livestock grazing.

Collection of vegetation data

Three methods were used to monitor different aspects of the vegetation development in the study site: permanent transects, vegetation mapping based on aerial photographs and sampling plots representing treatment groups of the experimental design. To monitor the presence of target

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species at the study site, three permanent transects (100 m in width and a length of 250–310 m) were set up at a perpendicular angle to the coastline in the year before de-embankment. Transect 1 was located in the higher-elevation western part of the study site, and the other two transects were located in the lower-elevation parts in the centre and to the east (Fig. 1). These three permanent transects were scored for species occurrence in August of the year before de-embankment, and years 1 to 4, 6 and 10 after de-embankment (2000, 2002–2005, 2007 and 2011) by recording the presence/absence of species in each 10 m × 10 m cell. Three pairs of species that were difficult to distinguish in the vegetative phase in the field were pooled in these categories: *Agrostis stolonifera*/*Alopecurus geniculatus*, *Juncus bufonius*/*J. ambiguus* and *Salicornia europaea* L./*S. procumbens* Sm.

The list of target species for this salt marsh was based on a modification of the regional species pool of Central North Atlantic European salt marshes as defined by Wolters et al. (2005). These authors compiled a list of 39 target species based on 22 salt marsh community types using the extensive Vegetation Classification surveys of the Netherlands of Schaminée et al. (1998) and a threshold of occurrence in 61% or more of the phytosociological relevés for each salt marsh community type. This list was shortened because not all the 22 salt marsh community types as described in Schaminée et al. (1998) are found in mainland salt marshes in the Netherlands. Furthermore, after consultation with one of the authors (M. Wolters pers. comm.), the following changes were made to the species target list based on the above-mentioned criterion: two species (*Odontites vernus* subsp. *serotinus* and *Phragmites australis*) were added, and three species (*Lotus corniculatus*, *Trifolium repens*, *Festuca arundinacea*) were removed. This resulted in a total of 23 target species for the study site (Appendix S1).

The temporal changes in the vegetation were monitored through comparison of vegetation maps of the study site over time. In addition to using existing vegetation maps from 14 yr before, and 1 and 7 yr after de-embankment in 2001 (1987, 2002 and 2008; Directorate-General of Public Works and Water Management, *Rijkswaterstaat*), we mapped the vegetation 10 yr after de-embankment from 9–16 Sept 2011 using the Previous Boundary Method (Janssen & van Gennip 2000; Janssen 2001). This method was developed in order to minimize chronological uncertainties in sequential mapping and is used as a standard procedure by *Rijkswaterstaat*. We applied this method using the boundaries in the 2008 vegetation map and aerial photographs from 2011. A handheld GPS (Trimble GeoXT) was used to check our position in the field. The community types in each map were then re-classified according to typology developed within the framework of the Trilateral Monitoring and Assessment Programme (TMAP) of the Wadden Sea between Denmark, Germany and the Netherlands (Esselink et al. 2009; Petersen et al. 2014). The TMAP types were simplified into broader categories: secondary pioneer marsh, low marsh, high marsh, brackish marsh and fresh grassland communities. 'Secondary pioneer marsh' was the term we used for the pioneer community found after disturbance, such as grazing and trampling, at higher elevations than expected by zonation in order to distinguish it from the primary pioneer marsh community that is normally found from 0.20 m below to around MHT. 'Fresh grassland' refers to grasslands that are not, or minimally, influenced by seawater and, therefore, lack halophytic plant species.

To test for the effects of the various factors in the experimental design on species composition, the cover for each plant species in the sampling plots was estimated using the decimal scale (Londo 1976). The three pairs of species pooled in the permanent transect data were distinguished as separate species here. The cover data from these 72 sampling plots were collected from mid-Jul to Aug 2011.

Collection of abiotic data

The elevation of the three permanent transects was measured in Sept/Oct 2003 (year 2) and in Sept 2011 for Transect 1 and in Apr 2012 for Transects 2 and 3 (year 10) using a theodolite (Leitz) or laser surveying equipment (Spectra precision laser, model LL500) and benchmarks linked to a fixed ordnance datum. Each 10 m × 10 m grid cell in the permanent transects was measured at four to six points, which were evenly placed over the area of the grid cell and avoided the drainage ditches. The depth of the drainage ditches was determined separately with at least two measurements per grid cell.

At each of the 72 sampling plots spread over 12 subsites, data were collected on elevation and salinity. Next to each plot, changes in surface elevation were monitored with sedimentation-erosion-bar (SEB) measurements (Nolte et al. 2013). A SEB point consisted of two horizontally aligned 1.5-m long poles 2 m apart (diameter = 7.5 cm) that had been inserted more than 1-m deep into the underlying sandy layer. The height of the poles was linked to a fixed ordinance datum, which was transformed into height above MHT. During elevation measurements, a 2-m long aluminium bar with 17 holes (10-cm apart) was placed horizontally on top of the two poles, and surface elevation was measured to the nearest millimetre by lowering a 50-cm long pin through each of the 17 holes down to the marsh surface. The mean of these 17 measurements represents one SEB data point. In 2011, these elevation measurements were taken during August and September.

Soil salinity was measured by collecting soil samples from all sampling plots during a single sampling on 1 Sept 2011. From each sampling plot, 12 subsamples were taken from the topsoil (0–5 cm), mixed and sealed in plastic bags for transport to the laboratory for further processing. Soil moisture content was measured by weight loss after drying the soil at 105 °C for 48 h. Salinity of water extracts was measured with a chloride-sensitive electrode after centrifuging the soil suspensions (15 g fresh soil, 50 ml distilled water; Hofstee 1983). Soil salinity was expressed as the concentration of chloride ions in the moisture contained in the soil (g·Cl^{-}·L^{-1} soil moisture).

Redox potential was also measured inside and outside the exclosure at ten of the 12 sub-sites for soil salinity in Sept 2011. Five platinum-tipped probes and an HgCl/KCl reference probe connected to a GL200 datalogger (Graphtec GB, Wrexham, UK) were inserted into the ground at three different soil depths (2, 5 and 10 cm). The data were then calibrated against three different pH solutions (pH = 4, 7 and 9). The data were pooled over the five probes and averaged over the three soil depths.

Statistical analysis

Multivariate analysis was used to determine the effect of experimental factors and other abiotic factors on species composition of the 72 sampling plots 10 yr after de-embankment. An initial detrended correspondence analysis (DCA) determined that the environmental gradient was very long (first axis was 4.48 SD units), so unimodal methods were more suitable than linear methods. Plant cover data derived from the decimal scale (Londo 1976) were transformed so that the total plant cover was equal to that estimated in the field for each sampling plot. Then the data were further transformed ($y = \log(x + 0.1)$) to prevent undue dominance by a few abundant species and to account for the high number of zeros in the data set.

Partial canonical correspondence analysis (CCA) and Monte Carlo permutation tests were used to test the significance of four models: (1) the full model including both nominal treatment variables and quantitative abiotic variables, (2) the experimental design model including only nominal variables, (3) the abiotic variables model including elevation and salinity, and (4) the parsimonious model containing only significant factors. Because the effects of elevation and salinity are very important from management perspectives, we did not remove their effects from the analysis either implicitly using multivariate analogues of randomized block designs (using spatial blocks) or explicitly using multivariate analogues of analysis of covariance. In the ordination diagrams, we chose the options of focus on sample scaling along with Hill's scaling type (Hill 1979) to optimize interpretation between sampling plots and display the species' point as the optimum of its unimodal response.

Since the experimental design model was orthogonal, we were able to use a multivariate analogue of ANOVA, which consisted of multiple CCA ordinations and associated Monte Carlo permutation tests. In unimodal methods such as CCA, *inertia* is used as the parameter to estimate variability. Inertia is a measure of variance related to the chi-square statistic (ter Braak & Šmilauer 1998). Eight separate significance tests using Monte Carlo permutation tests (499 permutations) were run for the analysis of inertia (ter Braak & Šmilauer 1998), including one for the full experimental design model (2 × 2 × 2 full factorial), three main effects (distance to breach, distance to creek, grazing treatment), three two-way interactions and one three-way interaction. Dummy variables (0, 1) were used to encode the nominal treatment factors. For the permutation tests when assessing main effects, the factor in question was used as the *environmental variable* and the other two factors were used as *covariables*. Permutations were restricted by blocks defined by all covariables. In the case of two-way interaction tests, all three factors were listed as covariables, and for the three-way interaction test, all three factors plus all three two-way interactions were used as covariables. Permutations for interaction effects were unrestricted. When a factor is used as a covariable in an analysis, only the variance explained by the environmental variables after subtracting overlapping variance attributable to the covariables is considered. All multivariate analyses were conducted using CANOCO (v 4.5; Microcomputer Power, Ithaca, NY, US).

Results

Target species

In the year before de-embankment, the percentage of 23 target species recorded in the permanent transects varied from 35% in the high-elevation transect (T1) to 70% in the low-elevation transects (T2 and T3; Fig. 2). In the high-elevation transect located in the west of the study site, the percentage of target species recorded had already reached a high of 83% by the third year after de-embankment. The relative gain in target species was less in the low-elevation transects, but the transect (T3) with the lowest average elevation contained almost all the target species by year 10 after de-embankment. T3, however, also had higher variation in elevation than T2 (van Duin et al. 2007). The initial differences in height between the high-elevation and two low-elevation transects were still present 10 to 11 yr after de-embankment, although the surface elevation change and filling of the ditches were higher in the low-elevation transects (Table 1).

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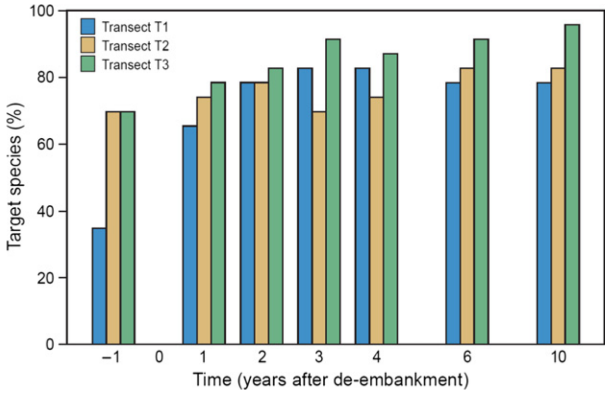

Fig. 2. The percentage of the target species recorded in the three permanent transects increased after de-embankment and reached very high values within 10 yr. Transect 1 was located at high elevations, and Transects 2 and 3 were located at low elevations. The 23 target species are identified in Appendix S1.

Changes in the vegetation

Before de-embankment, all of the experimental area was covered with the fresh grassland community (Fig. 3a). One year after de-embankment, this community was already reduced to less than a third of the area, and had disappeared completely after 10 yr. The largest increase in area was observed for the secondary pioneer marsh community dominated by highly salt-tolerant annuals. By year 10 after de-embankment, this community occupied about half of the experimental area. The low-marsh community increased to 17% of the area 1 yr after de-embankment and remained relatively constant thereafter. The high-marsh community increased slowly from 12% 1 yr after de-embankment to 24% after 10 yr. The area occupied by the brackish marsh community was variable over the years and never reached more than 21%.

The vegetation map of the study site made 10 yr after de-embankment shows the spatial distribution of the plant communities over the area (Fig. 3b). The low-elevation areas to the east were dominated by the secondary pioneer community, whereas the high-elevation areas to the west were covered by a progression of the low-marsh, brackish marsh and high-marsh communities from east to west. The low-marsh community was found in the central part of the area and along the creek banks in the low-elevation part to the east. An intermittent border of the high-marsh community ran along the landward edge of the experimental area. The differences in elevation between the eastern and western areas were also linked to differences in drainage: ditches in the low-elevation areas filled more rapidly over time causing these ditches to be less effective in draining away tidal water compared to the ditches in the high-elevation areas to the west (Table 1).

Factors influencing species composition in the sampling plots

Significant factors for species composition 10 yr after de-embankment are presented here. The experimental design model was able to account for 29.0% of the variability in the species data (Appendix S2). All the main effects of factors were statistically significant and grazing treatment explained the most variance, followed by distance to creek and distance to breach (Table 2). Note that grazing also had a very strong effect on soil redox potential with aerated soils found under ungrazed sampling plots and saturated soils found under grazed sampling plots (Table 3a). This effect on redox potential was stronger than that exerted by proximity to a creek. However, the interaction between distance to creek and grazing treatment was also significant, so the main effects for these factors will be disregarded in the interpretation of the results. The other two two-way and the three-way interactions were not statistically significant, and were not included in the parsimonious model. The abiotic variables model accounted for 20.9% of the species variability (Appendix S2). Within this model, elevation accounted for 14.3%, salinity accounted for 16.0% and there was 9.3% overlap between the species variability accounted for by these two factors.

The ordination diagram of the parsimonious model in Fig. 4 illustrates the relationship between elevation and salinity, the sampling plots, species composition and significant treatment classes (interaction between distance to creek and grazing treatment). The treatment classes for distance to breach were also significant, but they are not shown in the ordination as they explained very little variation and clustered very closely around the origin. The parsimonious model explained 42.4% of the species

Table 1. Mean values of marsh surface elevation and depth of ditches in the three permanent transects 2 and 10 yr after de-embankment.

Transect	Elevation (m +MHT)		Drainage Ditch Depths (cm)	
	2 yr	10 yr	2 yr	10 yr
T1	0.63 ± 0.004 (236)	0.66 ± 0.004 (239)	10.1 ± 0.37 (160)	5.8 ± 0.23 (170)
T2	0.45 ± 0.003 (254)	0.52 ± 0.003 (257)	11.3 ± 0.37 (195)	2.7 ± 0.19 (197)
T3	0.43 ± 0.003 (310)	0.50 ± 0.003 (310)	10.3 ± 0.29 (245)	2.9 ± 0.36 (229)

MHT = Mean High Tide, variability (±) is expressed in SE, numbers in parentheses represent sample sizes.

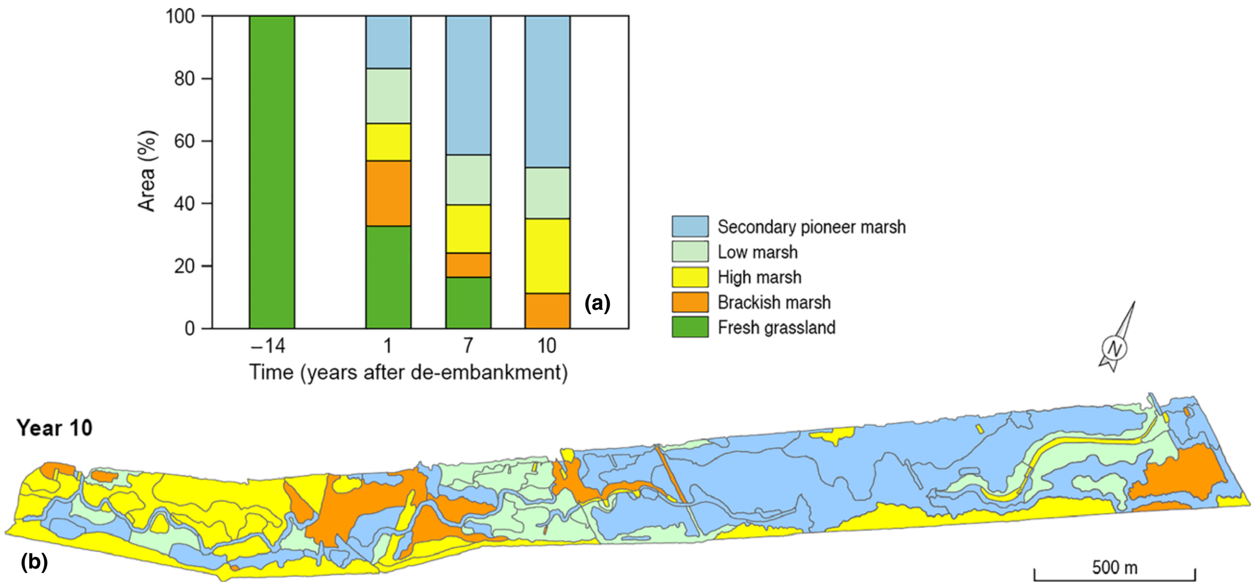

Fig. 3. (**a**) Changes in the relative area covered by different plant communities. The vegetation changed from the fresh (anthropogenic) grassland community to almost 50% secondary pioneer marsh community by 10 yr after de-embankment. (**b**) Vegetation map of the different plant communities in year 10. The secondary pioneer marsh community covered most of the lower elevated eastern half of the study site, whereas the high-marsh community established mainly in the higher elevation western half.

Table 2. The interaction between distance to creek and grazing treatment, and the main effect of distance to breach were the most significant factors in the experimental design model: multi-species analysis of inertia using partial CCA and Monte Carlo permutation tests (499 permutations). The experimental design model accounted for 29.0% of the inertia, which is a measure of variance related to the chi-square statistic.

Source of Inertia	*df*	Inertia Explained (%)	*F*-Ratio	*P*-Value
Distance to Breach	1	0.093 (4.9)	4.055	0.002
Distance to Creek	1	0.135 (7.0)	5.891	0.002
Grazing Treatment	1	0.154 (8.0)	6.738	0.002
Breach × Creek	1	0.021 (1.1)	0.938	0.460 n.s.
Breach × Grazing	1	0.024 (1.2)	1.071	0.326 n.s.
Creek × Grazing	1	0.106 (5.5)	4.884	0.002
Breach × Creek × Grazing	1	0.021 (1.1)	0.960	0.442 n.s.
Residual	64	1.357		
Total	71	1.911		

n.s. = not significant.

Table 3. Soil redox potential (mV, mean ± SE) under (a) different treatment classes (distance from creek and grazing) and (b) different plant communities. Values represent the average value at three soil depths (2, 5 and 10 cm).

(a) Treatment (*N* = 20)			
Creek Far & Grazed	Creek Far & Ungrazed	Creek Near & Grazed	Creek Near & Ungrazed
−167.4 ± 102.4	222.2 ± 71.3	−182.7 ± 59.8	255.6 ± 73.0
(b) Plant Community			
Secondary Pioneer Marsh (*N* = 2)	Low Marsh (*N* = 2)	Brackish Marsh (*N* = 2)	High Marsh (*N* = 14)
−348.9 ± 108.2	−264.7 ± 1.6	−266.3 ± 50.4	171.3 ± 47.2

variability (Appendix S2). The significant main effects of distance to creek and grazing treatment were also included in the parsimonious model, but the centroids of these treatment classes are not shown in the ordination as their interaction effect was significant. The first CCA axis explained 22.2% of the species variability, and CCA scores

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clearly decreased with elevation (inter-set correlation = −0.69) and increased with salinity (inter-set correlation = 0.76).

Plot distribution along axis 1 indicated a progression from the secondary pioneer marsh community to the low-marsh community to the high-marsh and brackish marsh communities from the right (high salinity/low elevation) to the left (low salinity/high elevation; Fig. 4). Six grazed sampling plots located far from creeks (CfG) with high salinity and low elevation clearly form a secondary pioneer marsh group at the right of the ordination. They were associated with highly salt-tolerant annuals such as *Salicornia europaea, Suaeda maritima* and to a lesser extent, *Salicornia procumbens* and *Spergularia salina*. These sampling plots of the secondary pioneer marsh community also had the lowest redox values (Table 3b), which indicates poor drainage and subsequent waterlogging. The second CCA axis explained 10.6% of the variability in the species data and appeared to be weakly related to grazing treatment and the

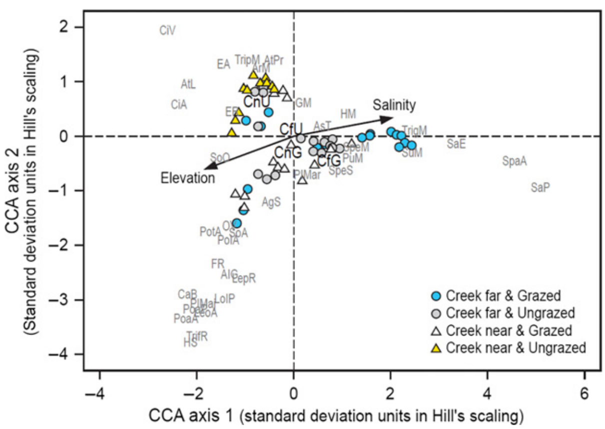

Fig. 4. Ordination diagram of the parsimonious model shows that, 10 yr after de-embankment, grazing far from creeks at low elevations results in the secondary pioneer community with *Salicornia europaea* (SaE) and *Suaeda maritima* (SuM), and lack of grazing near creeks results in the high-marsh community with *Elytrigia repens* (ER) and *Artemisia maritima* (ArM). CCA is constrained by the experimental design (main effects of distance to breach, distance to creek, grazing treatment, and distance to creek × grazing treatment interaction) and two continuous abiotic variables (elevation and salinity). The centroids of the interaction treatment classes between distance to creek and grazing are shown with large black letters (C = creek, f = far, n = near, G = grazed and UG = ungrazed). Symbols representing samples are also illustrated by their membership in treatment classes and are explained in the inset legend. The arrows representing the abiotic variables have been magnified five times. Hill's scaling with a focus on sample distances was used. The small grey letters represent species, and most of the abbreviations are explained in Appendix S1. Abbreviations of species not found in Appendix S1 are given here: CaB = *Capsella bursa-pastoris*, LepR = *Lepidium ruderale*, PoaA = *Poa annua*, PoaP = *Poa pratensis*, SaE = *Salicornia europaea*, SaP = *Salicornia procumbens*, SoA = *Sonchus asper*, SoO = *Sonchus oleraceus*.

distance to a breach point. Ungrazed sampling plots located near creeks (CnUG), which always had high elevation and low salinity values, were always covered by the high-marsh community associated with *Elytrigia repens, Atriplex prostrata* and *Artemisia maritima*. The high-marsh community also had the highest redox values (Table 3b), which indicates relatively high aeration of soil. The last two classes of interaction treatments between grazing and distance to creek (CnG and CfUG) resulted in more variable outcomes with respect to species composition. For example, when grazing was applied near a creek, the low-marsh community dominated by *Puccinellia maritima* developed where elevation was lower. At higher elevations, this combination of treatments resulted in either the high-marsh community dominated by *Elytrigia repens* or the brackish marsh community dominated by *Agrostis stolonifera* after 10 yr.

The main effect of the distance to a breach point was statistically significant but explained very little of the species variation (Table 2). In contrast, the interaction treatment classes between grazing and distance to creek were easier to interpret. The centroid for the ungrazed treatments located near to creeks (CnU) was clearly separated from the other three treatment classes. This treatment class was associated with typical high-marsh species such as *Elytrigia repens*, *Artemisia maritima* and *Atriplex prostrata*.

Discussion

Highly successful establishment of target species in the restoration site

The saturation of the target species list (23 species) was very high at the study site (Fig. 2). Before de-embankment, 70% of the target species were already present at the site, and the percentage of target species present rapidly increased within 1 to 2 yr after re-exposure to tidal water. Only one target species, *Phragmites australis,* was not found in the permanent transects, but it was found elsewhere in the restoration site from year 6 after de-embankment onwards (Esselink et al. 2015). The significant presence of halophytes before de-embankment at this site was very likely due to the import of diaspores by seawater, either by occasional flooding over the summer dike during storm surges or via intrusion through culverts. The last tidal inundation of the summer polder before de-embankment was in Feb 1999. As a result of this occasional influx of diaspores, 12 target species were recorded in the soil seed bank (top 0–5 cm of soil) of the summer polder 4 yr before de-embankment in spring 1997 (Bakker et al. 2002). Also in 1997, two tidal culverts were opened permanently allowing for a limited but regular tidal exchange between the summer polder and the seaward salt marsh as a preparatory measure for de-embankment. These factors facilitated seed availability within the site, which may explain the limited effect of distance to breach on species composition 10 yr after de-embankment at NFB, in contrast to expectations.

The saturation level of the target species list is very high compared to those estimated by Wolters et al. (2005) in their review of 70 de-embankment sites. However, part of this was due to methodology, as we tailored the target species list to better reflect the potential salt marsh communities that could develop at our restoration site, i.e. mainland salt marshes on the coast of the Netherlands. Accessibility to seeds from a source area has been identified as a potentially important factor in colonization by target species. For example, at a restoration site in southwest Netherlands, where incoming tidal water flows over the seed source area, nearly all target species were present within a few years after de-embankment (Bakker et al. 2002). However, there are cases for which the distance between the restoration site and source area did not seem to be the most important factor in colonization by target species (Wolters et al. 2005), and a review of 18 de-embankment sites in the UK concluded that there was no correlation between distance to a natural marsh and the fraction of target species found at the restoration site (Mossman et al. 2012).

Qualified success in creating diverse salt marsh communities

The most dramatic result was the large, almost homogeneous area covered by the secondary pioneer marsh community in the low-elevation half of the study site by year 7 after de-embankment, with some further expansion by year 10 (Fig. 3). With respect to elevation within tidal frame, the pioneer marsh community generally develops between 0.20 m below MHT to around MHT in natural salt marshes. In artificial salt marshes, enhanced drainage can lower this to 0.40 to 0.20 m below MHT (Bakker et al. 2002). The mean elevation of the area covered by the secondary pioneer community at NFB, however, was 0.50 m above MHT 10 yr after de-embankment. Similar results were also found at managed re-alignment sites in the UK, where areas with elevations usually supporting the low-marsh community were dominated by bare ground and annual pioneer species (Mossman et al. 2012; Brooks et al. 2015). These sites were not grazed, but low redox potential was identified as the fundamental reason for this development.

Another important development was the steady increase of the high-marsh community over time, which doubled from 12% 1 yr after de-embankment to 24% after 10 yr. Without management intervention, the high-marsh community dominated by *Elytrigia repens* is predicted to be replaced by that dominated by *Elytrigia atherica*, which under the current conditions represents the final stage of salt marsh succession (Bakker et al. 2003). *E. atherica* was first recorded in the sampling plots 2 yr after de-embankment, present in 20% of the exclosed plots by year 4 and in 33% of these by year 10 (Esselink et al. 2015). *E. atherica* forms tall, dense stands with a thick litter layer, precluding establishment and growth of most other plant species. Unconstrained and widespread development of the high-marsh community would ultimately decrease both percentage of target species and diversity of salt marsh communities.

Importance of distance to creek × grazing treatment, elevation and salinity

In contrast to predictions, areas far from creeks and grazed areas did not always support species with high waterlogging tolerance, nor did ungrazed areas always support competitive species, such as *Elytrigia repens* and *E. atherica*. In fact, it was the interaction between distance to creek and grazing treatment that best accounted for differences in species composition. Exclusion of grazing next to creeks always resulted in development of the high-marsh community. In addition, this combination of treatment classes was always associated with higher elevation and lower salinity. Indeed, ungrazed sites in our study area have been shown to develop significantly higher elevation and lower salinity than grazed sites (Veeneklaas et al. 2015), which is linked to both sediment accretion and compaction processes (Esselink et al. 2015). In addition, grazing had a stronger influence on soil aeration than proximity to creeks, and only the high-marsh community had positive redox potentials (Table 3). Thus, the prognosis for ungrazed vegetation developing on well-drained soils is very clear. Unless sedimentation rates decrease or there is limited influence of salt water, succession is predicted to result in the high-marsh community dominated by *Elytrigia atherica* when salt marsh vegetation is not grazed by livestock, which will eventually result in the loss of target species (Bakker et al. 2003).

Applying livestock grazing next to creeks or lack of grazing far from creeks resulted in more variable outcomes depending on elevation: low-marsh community, brackish marsh community or high-marsh community. Grazed salt marshes have often been reported to have higher species diversity over time (Bakker et al. 2003; Wolters et al. 2005); however Wanner et al. (2014) concluded that this effect is scale-dependent because at larger scales, abiotic heterogeneity will prevent total dominance of a few tall-growing plant species. Furthermore, the effect of livestock grazing will also depend on soil texture and moisture as grazing by large herbivores is accompanied by trampling effects (Schrama et al. 2013). Especially on clay soils and

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under wet conditions, soil compaction by livestock can lead to higher water-filled soil porosity and low soil redox potentials. When grazing was applied to low-elevation areas far from creeks in our study, it always resulted in development of the secondary pioneer community, with higher soil salinity, and lower elevation and redox potential than the other community types. The interaction between grazing and soil drainage conditions was also found when changes in management were applied to an artificial salt marsh in the Ems estuary on the border between northern Netherlands and Germany. Abandonment of the artificial drainage ditches led to increased waterlogging, which reinforced the trampling effects of grazing and favoured secondary pioneer vegetation (Esselink et al. 2002).

The long-term prognosis for the areas covered by the secondary pioneer community is potentially positive because successional processes will likely result in trajectories beyond this stage. However, the outcome and time scales of these successional trajectories will depend on a number of factors. As sediment deposition at the de-embanked site is still lower than in the bordering salt marsh (Esselink et al. 2015), the study site is likely to remain situated in a depression with relatively long inundation periods after tidal flooding. The observed strong interaction between soil waterlogging and livestock grazing implies that an adaptation to the management by a considerable reduction of the grazing intensity, for instance by the introduction of fallow years, would result in a decrease of the secondary pioneer marsh community covering this site.

Implications for ecosystem function and management

With respect to ecosystem function, what were the consequences of these vegetation changes after de-embankment for providing habitat for different groups of species? NFB is an important staging site for migratory Barnacle and Brent geese. A study conducted on goose utilisation of this site measured both a decrease in food plants available for geese and lower utilisation of the restored site after de-embankment (Bos et al. 2014). NFB is also an important habitat for breeding bird species, and some of these species have been identified as having declining populations, e.g. Common redshank, Oystercatcher, Pied avocet, Black-tailed godwit. In a study conducted over the mainland salt marshes in the Netherlands, both species richness and breeding bird density generally increased with the percentage of tall vegetation present on a salt marsh when data for all species were pooled (Mandema et al. 2015).

In conclusion, it must be considered that the restoration goals are actually aimed at 'moving targets' in that NFB is clearly still undergoing successional processes. Management regimes should be geared to directing the system towards desirable successional trajectories. To increase the compositional and structural diversity of salt marsh vegetation in high, well-drained areas, we advise grazing regimes that vary livestock type, stocking density and periodicity (including an ungrazed treatment). To prevent extensive formation of secondary pioneer marsh in low areas, we suggest two alternative or complementary scenarios: (1) conserving or retaining the existing drainage network before de-embankment; and (2) delaying livestock grazing or applying rotational grazing with one or more fallow years to allow for recovery. To avoid trampling effects, rotational grazing is preferred over continuous grazing at low stocking densities. Furthermore, increasing topographic heterogeneity would likely result in more heterogeneous vegetation with higher functionality.

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Supporting Information

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

Appendix S1. Changes in the frequency of species in the three permanent transects over time.

Appendix S2. Multivariate models for factorial experiment.