



Long-term management is needed for conserving plant diversity in a Wadden Sea salt marsh

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Abstract

Evaluation of long-term management regimes is important for guiding biodiversity conservation in salt marshes. However, such long-term experiments are sparse. Using a 46-year experiment in a salt marsh, we evaluated long-term effects of eight different management regimes (treatments; control, grazing, mowing, and their combinations) on the expansion of a late successional plant species (*Elytrigia atherica*), plant species richness and diversity, and community composition (species identities and dominance structure). Results show that *E. atherica* expanded strongly over time in the control treatment (without grazing or mowing) while plant species richness and diversity declined substantially. By contrast, *E. atherica* was greatly suppressed while plant species richness and diversity remained relatively unchanged in all other treatments except for the mowing, where species richness declined in the late season mowing treatment and plant diversity declined after 17 years in the both early and late season mowing treatment. Therefore, all management types except for the mowing were effective in conserving plant diversity. The trends for change in species identities reversed: change in species identities accumulated in the control treatment and exceeded that of other treatments 15 years after the start of the experiment. This suggests that results based on shorter-term (< 15 years) experiments may provide misleading conservation recommendations. Also, trends for change in dominance structure (taking abundance into account) were substantially different from those for species identities. Our results highlight the importance of long-term monitoring for guiding conservation management, and that monitoring should not only focus on the number of species but also community composition, to fully identify critical changes.

Keywords Grazing · Livestock · Mowing · Vegetation succession · Community composition

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Introduction

Grazing and mowing are among the most widely used management tools for conserving biodiversity in terrestrial grasslands and salt marshes worldwide (Davidson et al. 2017; Gedan et al. 2009; Tälle et al. 2016). The effects of grazing on plant and insect communities (diversity and composition) have been well-documented in salt marshes (Bakker et al. 2019; Bos et al. 2002; Burkepile et al. 2017; Ford et al. 2013; Kiehl et al. 1996; Pétilion et al. 2007; Rickert et al. 2012; Van Klink et al. 2016). However, mowing has become less common in salt marshes in recent decades (Bakker et al. 2002b; Gedan et al. 2009; but see Bakker 1978; Pétilion et al. 2007). Short-term studies (<15 years) from terrestrial grasslands comparing grazing and mowing (yearly) on plant diversity show inconsistent results. Some studies show that grazing is better than mowing (Bakker 1985; De Cauwer and Reheul 2009; During and Willems 1984; Fritch et al. 2011; Herbst et al. 2013; Jacquemyn et al. 2003), some show that mowing is better than grazing (Catorci et al. 2014; Stammel et al. 2003; Tälle et al. 2015), while others show that both have similar effects (e.g. Wellstein et al. 2007). Also, results from grasslands suggest the timing and frequency of mowing can modify the effects of mowing on plant diversity (Bakker et al. 2002a; De Cauwer and Reheul 2009; Dee et al. 2016). To our knowledge, studies, particularly the long-term ones (decades long), from salt marshes comparing grazing, different timing and frequency of mowing, and their combinations on plant diversity are rare.

The Wadden Sea salt marshes, representing ca. 20% of the total coastal salt marshes in Europe (Esselink et al. 2017), have traditionally been used for livestock grazing and, to a lesser extent, mowing (haymaking) (Bakker et al. 2002b). In the past decades, livestock grazing reduced or ceased in salt marshes as agriculture and economic interest decreased while conservation interest gained in importance (Bakker et al. 2003). However, cessation of grazing led to the local dominance, for instance, by the late successional tall grass, *Elytrigia atherica* (synonym *Elymus athericus*), particularly in the higher marshes (Veeneklaas et al. 2013), or *Atriplex portulacoides* in the lower marshes (Wanner et al. 2014), or *Phragmites australis* in brackish coastal marshes (Sammul et al. 2012). Increased dominance is usually accompanied by a decline in plant diversity (Koerner et al. 2018), which in turn can reduce ecosystem functioning, for instance, lower productivity (Tilman et al. 2001) and resilience to climate extremes or other anthropogenic environmental changes (Hautier et al. 2015; Isbell et al. 2015). To reverse this trend, different management regimes, usually focusing on different grazers and grazing intensity, were introduced (e.g. Bakker et al. 2019; Van Klink et al. 2016; Wanner et al. 2014). However, which management (including not only grazing but also mowing) is optimal for conserving biodiversity in salt marshes, particularly in the long term, remains debated (e.g. Van Klink et al. 2016).

Using a 46-year experiment in a Wadden Sea salt marsh, we evaluated the long-term effects of different management regimes (undisturbed control, grazing, early and late season mowing, and their combinations) on the expansion of the dominant grass *E. atherica*, plant species richness and diversity. Also, we evaluated these effects on community composition (species identities and dominance structure), given that the identities and abundance of the plant species can sometimes be as important as diversity in delivering ecosystem functioning and services (e.g. Winfree et al. 2015).

Materials and methods

Study site and experimental design

The Wadden Sea salt marshes have high conservation value as they harbor a wealth of plant and animal species, some of which are endemic to this area. These salt marshes are therefore protected under the EU Habitats Directive (EC Habitats Directive 1992). The experiment was conducted in one of these salt marshes, the natural high productive ($1120 \pm 201 \text{ g dw m}^{-2}$; mean $\pm 1 \text{ se}$; measured in 2018) salt marsh in the barrier island of Schiermonnikoog ($53^\circ 30' \text{ N}$, $6^\circ 10' \text{ E}$), the Netherlands (Bakker 1985). A small western part of the salt marsh had been grazed by cattle up to 1958 when grazing stopped. Cessation of grazing led to the local dominance of the tall late successional grass, *E. atherica*, which led to a decline in plant diversity over the following 10 years (Bakker 1985). The conservation managers wanted to reverse this trend. Hence, a field experiment to guide management practices started in 1972 in this area.

Four blocks were established in 1972, encompassing different plant communities characterized by different dominant species: block (1) *Festuca rubra* and *Armeria maritima*; block (2) *E. atherica*; block (3) *F. rubra* and *Artemisia maritima*; block (4) *F. rubra* and *Limonium vulgare*. Block 1 and 2 were situated in high marsh, block 3 and 4 in the low marsh. Enclosures (ca. $8 \text{ m} \times 42 \text{ m}$) within blocks, consisted of two electrical metal strands running 0.5 and 1 m above ground supported by wooden posts every 3.5 m. Note that small herbivores like hares, geese, and insects could enter the enclosures freely. Hares and geese can substantially slow down species decline over time particularly when their abundance is high (Chen et al. 2019). A previous study using this experiment shows that cattle grazing facilitates hare grazing, and possibly also goose grazing, because cattle graze down the tall grass *E. atherica*, which in turn promotes *F. rubra* favored by hares and geese (Kuijper et al. 2008). Each block contained eight different treatments, including (1) an undisturbed control (C, i.e. natural succession without grazing and mowing), (2) early season mowing (M (E)), (3) late season mowing (M (L)), (4) both early and late season mowing (M (EL)), (5) grazing by cattle (G), (6) grazing plus early season mowing (G + M (E)), (7) grazing plus late season mowing (G + M (L)), (8) grazing plus both early and late season mowing (G + M (EL)) (plot size ca. 18 m^2 for mowing treatments; experimental design in Fig. S1). Treatments within blocks were randomized in the field. We usually mowed in late June or early July for the early season mowing, and in late August or early September for the late season mowing. We cut the vegetation to 2 cm above ground using a brush cutter. Plant material (including litter) was raked and collected, and dry weight was determined. Cattle grazing was continuous from May to November annually. Stocking density decreased from 1.5 to 0.5 head ha^{-1} from 1993 onwards, as the cattle-grazed area increased (Bakker et al. 1993; Bos et al. 2002; Fig. S1). One permanent plot ($2 \text{ m} \times 2 \text{ m}$) for each treatment was established in 1972. We recorded species occurrence and abundance in the permanent plots before the start of mowing from 1972 to 2017. We used the data from 1972, 1974–1980, 1984–1989, 2003, 2015 and 2017, as all the eight treatments were measured in those years (thus 17 years of surveys). We estimated abundance (percent cover) using the decimal scale of Londo (1976). As we estimated percent cover for each species independently, the total cover of living plants can sometimes exceed 100% for the multilayer canopies. Plant species occurrence and abundance were recorded by a skilled field assistant for most years. A list of plant species occurred during the 46-year experiment can be found in Table S1.

Data analysis

Elytrigia atherica, *Festuca rubra*, and dominance

We explored temporal trends of percent cover of *E. atherica* and *F. rubra* in different treatments. We included *F. rubra* as it is the most dominant intermediate successional species in this salt marsh, and is replaced by *E. atherica* as the marsh ages. To check whether the change in abundance of these two dominant grasses was the main cause for change in dominance, we also explored the temporal trends of dominance using the Berger–Parker dominance index, and 1–evenness. Berger–Parker dominance index is measured as the proportional abundance of the most abundant species. Evenness was calculated as $H/\ln(S)$, where H is Shannon’s diversity index, and S is species richness. Dominance calculated as 1–evenness takes the abundance of all species into account. Temporal trends of dominance were similar using the Berger–Parker dominance index and 1–evenness. We therefore only presented the result of the Berger–Parker dominance index in the main text.

Species richness and plant diversity

We explored temporal trends of species richness and plant diversity. Species richness was measured as the number of species recorded within each permanent plot. Plant diversity was measured as Shannon’s index (H), taking into account the abundance of each plant species.

Community composition (identities and dominance structure)

We focused on change in community composition relative to its initial state in each treatment, thus the stability of community composition. We compared a community (in a permanent plot) in each year with that of the starting year 1972. We explored change in community composition based on the species presence /absence data (identities), and abundance data (dominance structure). We used function `beta.pair` and `beta.pair.abund` from the R package `betapart` (Baselga and Orme 2012; Baselga 2013) for change in species identities and dominance structure, respectively. We specified Sørensen index and Bray–Curtis dissimilarity index in these two functions, respectively. For the change in species identities (ranging from 0 to 1), when it approaches 0, species identities in a community in a later year are completely the same as that of the community in 1972, and when it approaches 1, species identities are completely different. Similarly, for the dominance structure, 0 suggests that species identities and their abundances in a community in a later year are completely the same as that of the community in 1972, while 1 suggests that species identities and/or their abundances are completely different.

We used `gamm` models from package `mgcv` (Wood 2017) to fit the temporal trends. In all the models except for *E. atherica*, treatment was the fixed variable, and smooths were fitted for each treatment, with block and permanent plot as random variables. Temporal autocorrelation was adjusted using the `corCAR1` model for unevenly spaced time series data. For *E. atherica*, there were too many zeros (299 of 544) in the data, and currently, package `mgcv` has not implemented a `zero_inflated_beta` distribution. Another package, `brms` (Bürkner 2017), implements this distribution, however, it does not implement autocorrelation for unevenly spaced time series data. Therefore, for *E. atherica* (`gamm`) model, we used the averaged percent cover data (across four blocks). In this model, treatment was the fixed variable, smooths were fitted for each treatment, and no random variable was specified, while

autocorrelation was specified to each treatment. Percent cover of *E. atherica* was fourth-root transformed, and percent cover of *F. rubra* was square-root transformed before fitting the models to improve the normality of the residuals and homogeneity of variance. We used family quasipoisson for the species richness (count data) model to account for overdispersion. We extracted the parametric coefficients and smooth terms from these models to assess the overall effects (averaged across 46 years; Table S2) and over-time effects (the trends are significant when $p < 0.05$; Table S3) for the different treatments. For the overall effects, we particularly focused on comparing other treatments to the control, as the control treatment was treated as the reference in these models. Data analysis was performed using R 3.5.1 (R Core Team 2018).

Results

Elytrigia atherica, *Festuca rubra*, and dominance

Overall, compared with the control, *E. atherica* decreased significantly in all other treatments (estimated from gamm models using data across 46 years; Table S2). Over time, *E. atherica* expanded strongly in the control treatment, while it remained low in all other treatments (percent cover $< 20\%$ on average; Fig. 1a). Overall, compared with the control treatment, *F. rubra* increased in the mowing treatments (nearly significant in the both early and late season mowing treatment) (Table S2). Over time, *F. rubra* decreased in the control treatment, while it generally increased in all mowing treatments. It also increased in the grazing treatment, and the grazing plus both early and late season mowing after 2010 (Fig. 1b; Table S3). In general, the pattern of dominance matched well with those changes in *E. atherica* and *F. rubra*. Overall, compared with the control, dominance decreased significantly in all other treatments (Table S2). Over time, dominance increased in the control, and in the both early and late season mowing treatment (Fig. 1c; Table S3).

Plant species richness and diversity

Overall, compared with the control, species richness and plant diversity increased significantly in all other treatments (Table S2). Over time, species richness declined in the control and the late season mowing treatments, it remained relatively unchanged in other treatments, except for the grazing plus early season mowing treatment where species richness varied (Fig. 2a; Table S3). Over time, plant diversity decreased in the control, it also decreased in the both early and late season mowing treatment after 1989, it remained relatively unchanged in other treatments (Fig. 2b; Table S3).

Change in the species identities and dominance structure

Overall, compared with the control treatment, change in species identities did not differ significantly in the other treatments (Table S2). Over time, species identities changed substantially in all treatments except for the grazing plus mowing treatments. Particularly, species identities changed strongly (relative to its initial state) in the control treatment 15 years after the start of the experiment (Table S3; Fig. 3a). Overall, compared with the control treatment, the dominance structure was significantly higher in the grazing plus both early and late season mowing treatment (Table S2). Over time, the dominance structure changed substantially in

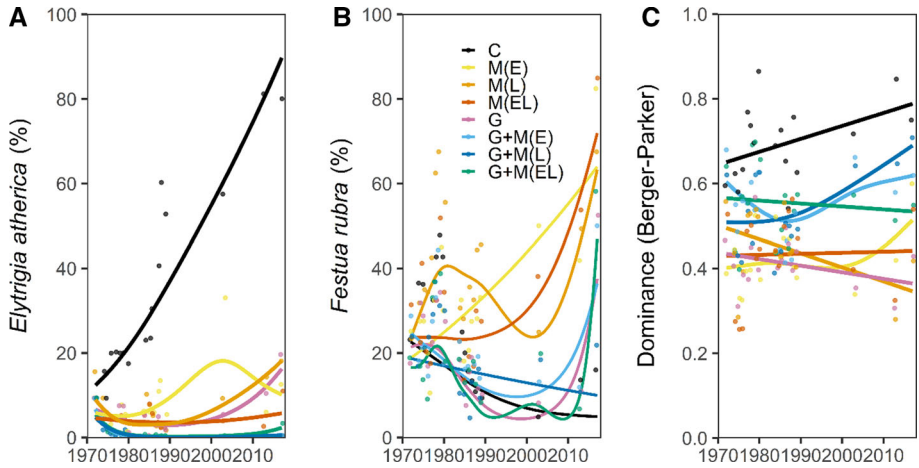


Fig. 1 Percent cover of *Elytrigia atherica*, *Festuca rubra* and dominance in different treatments during the 46-year experiment. Dots are the means of four blocks. Lines are fitted with generalized additive mixed model (gamm; Table S3). Berger–Parker dominance index is measured as the proportional abundance of the most abundant species. C: control, i.e. natural succession without grazing and mowing; M (E): early season mowing; M (L): late season mowing; M (EL): both early and late season mowing; G: cattle grazing; G + M (E): cattle grazing plus early season mowing; G + M (L): cattle grazing plus late season mowing; G + M (EL): cattle grazing plus both early and late season mowing

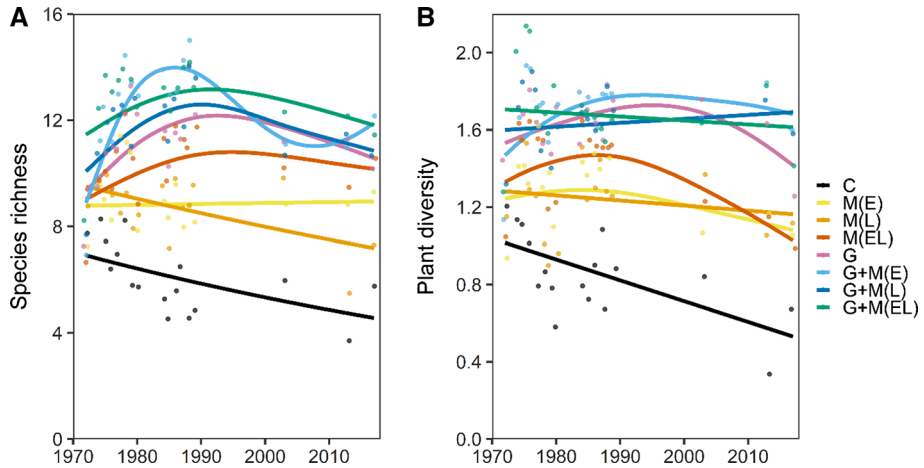


Fig. 2 Plant species richness and diversity in different treatments during the 46-year experiment. Dots are the means of four blocks. Lines are fitted with generalized additive mixed model (gamm; Table S3). Species richness was measured as the number of species recorded within the permanent plots (2 m × 2 m). Plant diversity was measured as Shannon’s index (H). Treatment description corresponds to that of Fig. 1

all treatments (Table S3; Fig. 3b), except for the grazing plus late season mowing treatments. It suggests that the plant species abundances were highly variable over time. Particularly, the dominance structure was much higher in the grazing plus both early and late season mowing treatment and, to a lesser extent, in the grazing plus early season mowing treatment than in the other treatments (Fig. 3b).

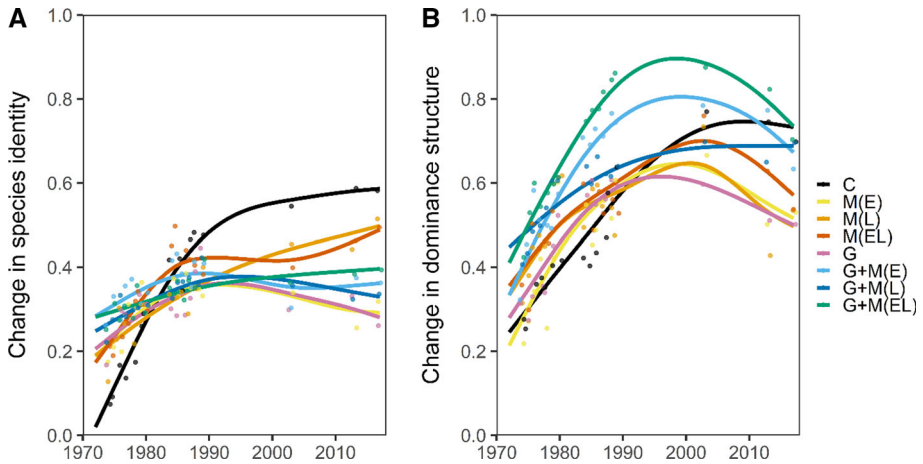


Fig. 3 Change in species identities and dominance structure in different treatments during the 46-year experiment. Dots are the means of four blocks. Lines are fitted with generalized additive mixed model (gamm; Table S3). For the change in species identities (ranging from 0 to 1), when it approaches 0, species identities in a community in a later year are completely the same as that of the community in 1972, when it approaches 1, species identities are completely different. Similarly, for the dominance structure, 0 suggests that species identities and their abundances in a community in a later year are completely the same as that of the community in 1972, while 1 suggests that species identities and/or their abundances are completely different. Treatment description corresponds to that of Fig. 1

Discussion

Our 46-year experiment evaluating long-term effects of eight different management regimes on plant communities suggests that long-term management is needed to suppress the expansion of the dominant grass *E. atherica*, and to conserve plant diversity in this salt-marsh ecosystem. Compared with the undisturbed control (without grazing or mowing), *E. atherica* was strongly suppressed in all other treatments while plant species richness and diversity remained relatively unchanged except for the mowing treatments. The trends for the change in species identities reversed: species identities in the control treatment changed less over time relative to its initial state in 1972 than any other treatments during the first 8 years, but changed more than all other treatments 15 years after the start of the experiment. In addition, the trends for change in dominance structure (taking abundance into account) were substantially different from those for change in species identities. Our results have important implications for plant diversity conservation in salt marshes. Our results also emphasize the importance of running experiments for long term to fully evaluate the effects of different management regimes on plant communities.

The dominance of *Elytrigia atherica*

In the control treatment, where no grazing or mowing management was imposed, *E. atherica* expanded strongly during the 46-year experiment. It suggests that in this salt marsh natural vegetation succession may lead to the dominance of this grass. Valéry et al. (2017) found that eutrophication (nitrogen enrichment) is the major driver of the rapid expansion of this grass in French salt marshes. However, Bockelmann and Neuhaus (1999) found that increasing nitrogen availability, similar to the amount of annual atmospheric input, does not significantly

impact the growth and expansion of *E. atherica* to the lower marsh in one of the Wadden Sea salt marshes. Also, Nolte et al. (2019) found that the increased elevation due to sediment accumulation, but not increased nitrogen availability, facilitates the expansion of *E. atherica* in another Wadden Sea salt marsh. Therefore, eutrophication may not play an important role in the expansion of this grass in Wadden Sea salt marshes. The block dominated by *E. atherica* at the start of this experiment remained dominated by this grass during the entire 46-year experiment (Fig. S2B). This indicates that the plant community dominated by *E. atherica* reaches a stable state. Increased dominance of *E. atherica* without disturbance has also been widely observed in other salt marshes across Europe (Milotić et al. 2010; Pétilion et al. 2005; Rupprecht et al. 2015; Van Klink et al. 2016; Wanner et al. 2014). This dominance of *E. atherica* in salt marshes is, however, undesired, as it leads to a decline in plant diversity. Compared with the control treatment, all other treatments substantially suppressed the dominant grass, *E. atherica*. Particularly, grazing plus any combination of mowing suppressed *E. atherica* the most in the block originally dominated by this grass 46 years after the start of the experiment (Fig. S2A). It suggests that for restoring plant communities dominated by this grass, grazing plus any combination of mowing may be more effective than grazing or mowing alone.

Species richness and plant diversity

Over time, plant species richness and diversity remained relatively unchanged in all treatments except for the control and mowing treatments. Species richness declined in the late season mowing treatment, plant diversity declined in both the early and late season mowing 17 years after the start of the experiment, likely due to the increased dominance (Fig. 1c; Koerner et al. 2018). Plant diversity also appeared to decline in the early season mowing and late season mowing treatment, although these trends were not statistically significant. These trends exist maybe because the intermediate successional grass, *F. rubra*, increased the dominance in these mowing treatments once the late successional grass *E. atherica* was suppressed (Fig. 1). However, different dominant species have different effects on species richness (During and Willems 1984). Wanner et al. (2014) demonstrated that species richness decreased by 2.5 species on average in 1-m² plots dominated (percent cover more than 30%) by *E. atherica* 20 years after the start of the experiment in a Wadden Sea salt marsh, while species richness decreased by less than 1 species on average in plots dominated by *F. rubra*. Lepš (2014) also reported that mowing was only able to mitigate plant species loss induced by fertilization in the short term in a 15-year field experiment in a species-rich grassland. Together, mowing may be a more suitable management tool for conserving plant diversity in the shorter term.

Community composition

Community composition based on presence/absence (species identities) and abundance data (dominance structure) showed different trends. Change in species identities remained relatively stable (relative to its initial state in 1972) over time in the grazing plus early season mowing, and the grazing plus both early and late season mowing treatments. However, the dominance structure in these two treatments changed substantially. This indicates that the species responsible for these changes were the more common or abundant species in these two treatments. This further suggests that small changes in the species identities can occur along with substantial changes in the dominance structure, which may substantially change ecosystem functioning (Winfree et al. 2015). Our results, therefore, support the idea that con-

ervation should not only monitor species richness but also include changes in community composition (e.g. Dornelas 2014; Hillebrand et al. 2018).

Effects of management regimes on environmental variables

Different treatments also had a different impact on environmental variables. In this study area, Schrama et al. (2013) found that, compared with the control and the late season mowing treatments, long-term cattle grazing strongly increases soil bulk density, increases carbon stock, while it reduces soil redox potential, soil macrofauna abundance, and nitrogen mineralization. This suggests that long-term cattle grazing—due to trampling, deposition of urine and dung—has profound effects on soil properties and nutrient cycling. In addition, these alterations of soil properties and nutrient cycling may have feedback on plant communities (Mikola et al. 2009), thus contribute to the observed changes in this experiment.

Comparing with salt marshes outside Europe

Compared with European salt marshes, livestock grazing is less common in America and Asia (Davidson et al. 2017; Gedan et al. 2009), while mowing is generally rare nowadays (Gedan et al. 2009). This makes it difficult to compare our results with salt marshes in America and Asia. The effects of grazing on plant diversity may be less apparent or negative in America (e.g. Wasson and Woolfolk 2011; Di Bella et al. 2014), because salt marshes in America are usually dominated by one or a few plant species (Conde et al. 2006; Pennings et al. 2001). By contrast, salt marshes in Europe harbor more plant diversity (Bakker et al. 2015). Also, grazing tends to decrease soil carbon stock in America, but not in Europe (Davidson et al. 2017). This may be due to different soil formation: European salt marshes are mainly derived from mineral deposition while American marshes are from organic material (Bakker et al. 2015). Hence, our results and implications for conservation management typically apply to European salt marshes.

To conclude, our results suggest that long-term experiments are important, and long-term management is needed to conserve plant diversity in this salt-marsh system. Overall, all the management regimes tested were effective in plant diversity conservation in this salt marsh. However, mowing may be more suitable in the shorter term. Grazing can substantially alter soil properties and nutrient cycling compared with mowing. Grazing plus early season mowing, and grazing plus both early and late season mowing may not be suitable if maintaining stability in the dominance structure is desired.

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Author contributions JB designed and conducted the experiments. CS and QC collected data since 2012, and 2016, respectively. QC and JA discussed the data analysis and set the conceptual framework of this manuscript. QC analyzed the data and wrote the manuscript. All authors contributed to the revisions and gave final approval for publication.

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