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Long-term vegetation dynamics after land-use change in Wadden Sea salt marshes

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Abstract

After the establishment of the National Park "Schleswig-Holstein Wadden Sea" in Northern Germany, sheep grazing was strongly reduced, or abandoned and the maintenance of the artificial drainage system in the abandoned areas neglected. We studied the long-term development of plant species density and evenness in salt marshes of the "Hamburger Hallig". In this area, a grazing experiment including intensively grazed, moderately grazed and abandoned plots, was established in 1991 and modified in 1995 and 1999. Species density increased on all permanent plots except for the high salt-marsh plots ungrazed since 1992, which had the highest species density of all plots in 1992 and showed a slight but non-significant decrease in species density between 1995 and 2004. In the intensively grazed salt marsh, the increase in species density was delayed until 1998. Vegetation evenness E1/D showed high inter-annual fluctuations with a strong decrease during the early years of the experiment but hardly any significant trend from 1995 to 2004. The decreasing species density between 1999 and 2004 on plots dominated by *Elymus athericus* indicated that this species was able to outcompete other species at high salt-marsh sites with well-aerated soils. In contrast, no decrease in species density could be observed on sites dominated by *Atriplex portulacoides*. In the low salt marsh and in less drained parts of the high salt marsh, soil water-logging and low sedimentation rates may impede large-scale species dominance and consequentially prevent a decrease in species density.

1 Introduction

Salt marshes are habitats with extreme environmental conditions due to regular flooding by seawater. Gradients of waterlogging and salinity from the pioneer zone over the low salt marsh to the high marsh induce a distinct vegetation zonation depending on the tolerance ranges of different plant species (Adam 1990). Intensive grazing of salt marshes by sheep or cattle can lead to a downward-shift of vegetation zones (Ranwell 1968, Bakker 1989) and to a loss of grazing-sensitive species because only a few plant species (e.g. *Salicornia* spp., *Puccinellia maritima*) tolerate frequent biomass loss and trampling (Kiehl et al. 1996). In the beginning of the 1990ies the vegetation of mainland salt marshes along the North Sea coast of Schleswig-Holstein (Northern Germany) was uniform with low structural diversity (Fig. 3) and characteristic grazing-sensitive species (e.g. *Atriplex portulacoides*) became endangered after decades of intensive sheep grazing (Kiehl et al. 1996, Stock et al. 1997).

After the establishment of the National Park "Schleswig-Holstein Wadden Sea", the formerly intensive sheep grazing in mainland salt marshes was strongly reduced or abandoned and the maintenance of the artificial drainage system was neglected in the abandoned areas (Stock 1997, Stock & Kiehl 2000, Bakker et al. 2005). To study the effects of different grazing intensities, large-scale experiments were established in different areas (Dierssen et al. 1997, Stock & Kiehl 2000). Short-term investigations showed that grazing-sensitive species were able to spread quickly within four or five years after grazing abandonment or reduction (Kiehl et al. 1996). During this period, plant species density was lowest in intensively grazed low salt marshes but did not differ between moderately grazed and ungrazed plots (Kiehl 1997). A meta-analysis of long-term vegetation changes in Wadden-Sea salt marshes showed, however, that grazing abandonment can have a negative effect on species density due to the dominance of competitive plant species such as *Elymus* spp. in the high marsh or *Atriplex portulacoides* in the low marsh (Bos et al. 2002). In contrast, some examples from long-term ungrazed salt marshes indicate that species-rich vegetation mosaics can also persist over long periods (Schwabe & Kratochwil 1984, Kiehl et al. 2000). The speed of vegetation succession in ungrazed Wadden-Sea salt marshes depends on drainage conditions and on sedimentation rates in relation to sea level rise (Leendertse et al. 1997, Olff et al. 1997, Schröder et al. 2002, Kiehl et al. 2003). In mainland salt marshes on clayey soils, species-poor stands of highly competitive Elymus spp. develop mainly at well-drained sites with high sedimentation rates and probably high nitrogen input (e.g. Andresen et al. 1991, Heinze et al. 1999), whereas soil water logging and high salinities can prevent dominance of single species on less drained sites with low sedimentation rates (Kiehl et al. 2003).

The aim of our study was to analyse long-term vegetation succession from 1992 to 2004 after the establishment of a large-scale grazing experiment in the salt marshes of the Hamburger Hallig. We addressed the following questions: i) What is the long-term effect of grazing reduction/cessation and of negleting the drainage system on species density and evenness of salt marsh vegetation? ii) Does species density decrease after grazing abandonment due to the spreading of potentially dominant species (e.g. *Elymus* spp., *Atriplex portulacoides*)? iii) What is the effect of large-scale abandonment on the vegetation of adjacent salt marshes, which are still intensively grazed?

2 Study area and methods

The salt marshes of the "Hamburger Hallig" (coordinates: 8° 51' E, 54° 37' N) are located in the National Park "Schleswig-Holstein Wadden Sea" and cover an area of 1047 ha (Stock et al. 2005). They have been grazed intensively by sheep (> 10 sheep ha^{-1}) until 1991. A grazing experiment including intensively grazed, moderately grazed and abandoned plots was established in 1991 and modified in 1995 and 1999 (Stock & Kiehl 2000, Schröder et al. 2002). In 1992, 38 permanent plots of 4 m² were installed in differently grazed areas of the salt marsh (Table 1). In 1995, seven additional plots were installed in the intensively grazed salt marsh because grazing had to be stopped for logistical reasons on those permanent plots, which had been grazed intensively from 1991 to 1994.

Table 1: Design of the grazing experiment: number of permanent plots in differently grazed parts of the salt marsh. All plots had been grazed intensively by sheep (> 10 sheep ha^{-1}) until 1991. Values in parentheses represent the number of plots from 1999 onwards, after two additional permanent plots had been installed near each of the "old" plots.

	Low salt marsh	High salt marsh	Total no. of plots
ungrazed since 1992	11 (33)	8 (24)	19 (57)
ungrazed since 1995 (grazed intensively by > 10 sheep ha^{-1} until 1994)	4 (12)	3 (9)	7 (21)
moderately grazed (1991-1994: 1.5 sheep ha^{-1}, 1995-2004: 0.75 sheep ha^{-1})	6 (18)	6 (18)	12 (36)
intensively grazed (> 10 sheep ha^{-1}), permanent plots installed in 1995	-	7 (21)	7 (21)
			45 (135)

After several years of succession, the vegetation became more heterogeneous than expected at the beginning of the experiment. To account for this spatial heterogeneity, two additional permanent plots were established in the direct vicinity of each of the already existing plots in 1999. So, in total 135 permanent plots were sampled at 45 locations from 1999 onwards.

The percentage cover of all plant species was estimated yearly on all permanent plots from 1992 to 2004 according to Londo (1976). Species density and the evenness index $E_{1/D}$ (Smith & Wilson 1996) with values between 0 (lowest evenness) and 1 (maximal evenness) were calculated for each year. Changes in species density and evenness were analysed for the 45 "old" permanent plots by a linear mixed effect model with plot as random effect and time and group as fixed effects. Analyses were computed by the lme function in the R package lme4 (Bates & Sarkar, version 0.9975-10). For these analyses, data from 1995 to 2004 were used, because the still intensively grazed plots were sampled first in 1995 (see above). Additionally, differences in species density between 1999 and 2004 were calculated for all 135 plots. To test for significant differences in changes of species density between 1999 and 2004 in relation to the species, which was dominant in 2004 (*Elymus athericus*, *Atriplex portulacoides*, *Festuca rubra*, *Puccinellia maritima* or *Spartina anglica*), the non-parametric Kruskal-Wallis H-test was used.

3 Results

3.1 Dynamics of species density and evenness under different grazing regimes

Species density increased on all permanent plots except for the high salt-marsh plots ungrazed since 1992, which had the highest species density of all plots at the beginning of the study (1992) and showed a slight but non-significant decrease in species density between 1995 and 2004 (Fig. 1, Tab. 2). On plots with similar grazing regime, the increase in species density was generally higher in the low salt marsh than in the high salt marsh. Within one salt marsh zone, the increase was more pronounced on continuously grazed plots and lowest on sites that became abandoned already in 1992 (Tab. 2). In the intensively grazed salt marsh, the increase in species density was delayed and only started in 1998 (Fig. 1).

Table 2: Rates of annual change in species density and evenness value between 1995 and 2004, estimated by a linear mixed model. Data represent means ± 1 standard error. Significant changes ($p < 0.05$) are marked by an asterix.

	Species density, mean change [no. of species year^{-1}]	Evenness, mean change [Evenness year^{-1}]
Low salt marsh ungrazed since 1992	0.19 ± 0.06 *	0.0013 ± 0.0038
Low salt marsh ungrazed since 1995	0.31 ± 0.07 *	-0.0071 ± 0.0050
Low salt marsh moderately grazed	0.43 ± 0.07 *	-0.0078 ± 0.0044
High salt marsh ungrazed since 1992	-0.05 ± 0.06	-0.0148 ± 0.0041 *
High salt marsh ungrazed since 1995	0.11 ± 0.08	-0.0205 ± 0.0055
High salt marsh moderately grazed	0.18 ± 0.07 *	-0.0076 ± 0.0044
High salt marsh intensively grazed	0.36 ± 0.04 *	-0.0044 ± 0.0030

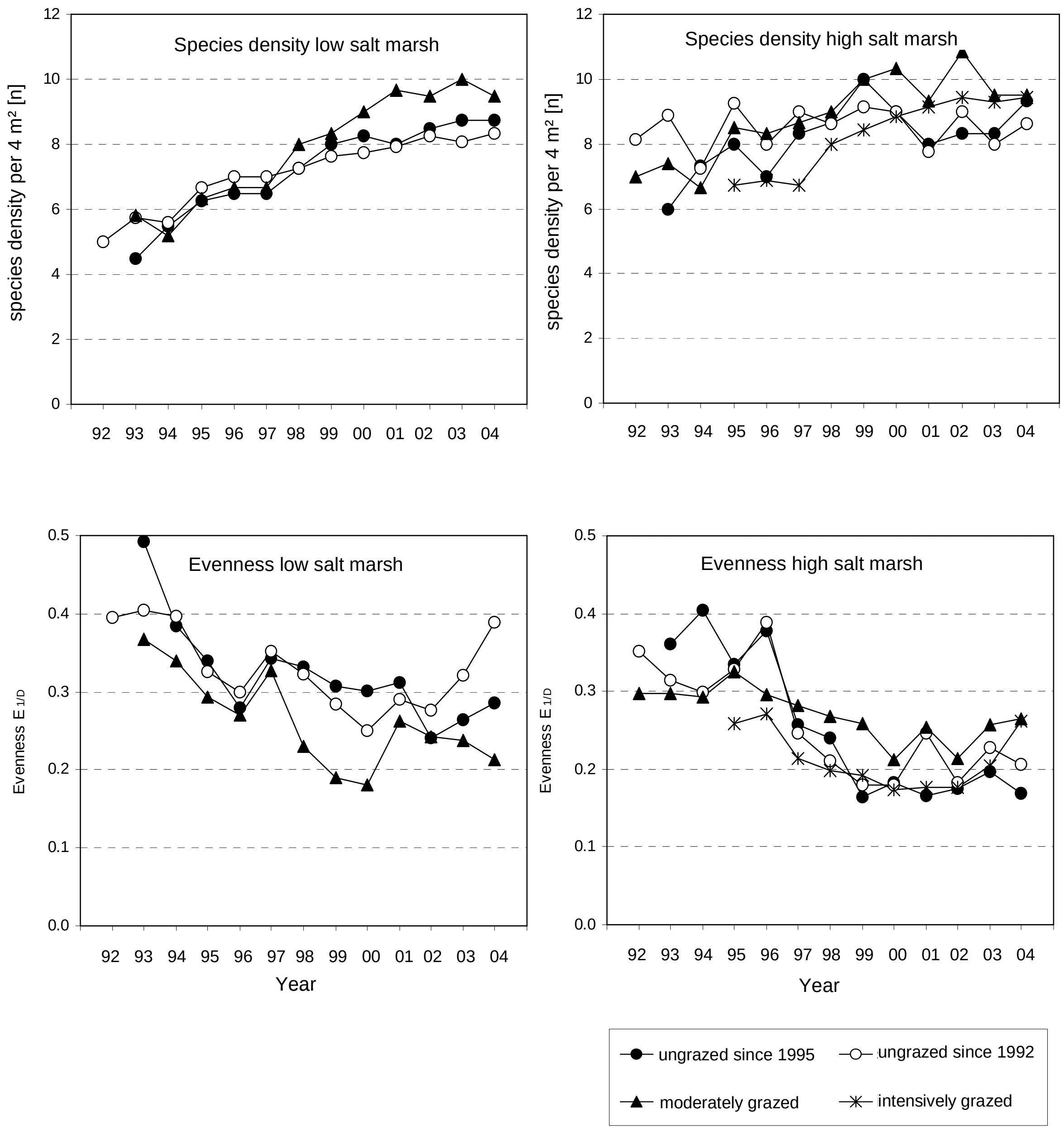

Figure 1: Changes in species density (4 m²) and evenness $E_{1/D}$ between 1992 and 2004 on differently grazed plots of the low salt marsh (left) and the high salt marsh (right).

Evenness values showed high inter-annual fluctuations with a strong decrease during the early years of the experiment but hardly any significant trend from 1995 to 2004 (Fig. 1, Tab. 2). Only in the ungrazed high salt marsh, a further decrease in evenness could be observed for this period.

3.2 What is the effect of dominant species on species density?

Species density decreased between 1999 and 2004 on most of the plots, which were dominated by *Elymus athericus* in 2004, but remained similar or showed even a slight increase on plots dominated by other species (Fig. 2). The decrease on plots dominated by *Elymus* was significantly different in comparison to the other plots ($p < 0.01$, $5 \leq n \leq 65$, df = 4, H-test). Only one plot dominated by *Elymus* showed an increase in species density between 1999 and 2004. No significant differences between median changes of species density were found between plots with dominance of *Atriplex portulacoides*, *Festuca rubra*, *Puccinellia maritima* or *Spartina anglica*.

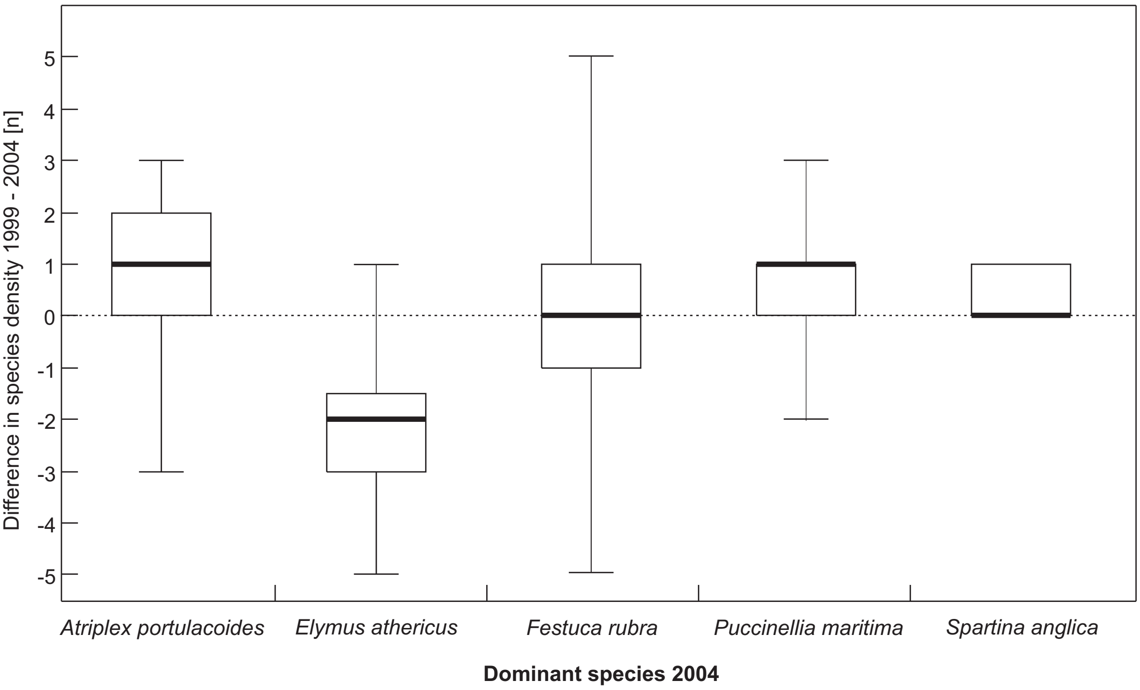

Figure 2: Difference in species density between 1999 and 2004 on permanent plots dominated by different plant species in 2004. Data represent medians (black line), upper and lower quartiles (box), minima and maxima (whiskers).

4 Discussion

Thirteen years after land-use change, species density in the salt marshes of the Hamburger Hallig increased considerably on most of the permanent plots due to the spreading of grazing-sensitive species (e.g. *Atriplex portulacoides*, *Artemisia maritima*). Up to now, a quick increase of these species after large-scale management change has been shown only for moderately grazed and ungrazed plots (Kiehl et al. 1996). During the early years after land-use change, species density remained low on intensively grazed plots because low seed availability and the selective grazing of the sheep hampered the colonisation of grazing-sensitive species (Kiehl 1997). In the present study, however, we found a delayed increase in species density even on formerly species-poor intensively grazed plots. This increase, which started seven years after the large scale land-use change in the study area (1998) and continued until 2004, was only possible because of the successful reproduction of grazing-sensitive species on adjacent moderately grazed and ungrazed plots (Fig. 4), which led to a high seed availability. As halophyte seeds are easily dispersed by flooding water (Koutstaal et al. 1987, Wolters et al. 2005) and no dispersal barriers exist in our study area, seed availability obviously became so high on the intensively grazed plots that the establishment of grazing-sensitive species was possible even under high grazing pressure.

A similar delayed increase in species density on intensively grazed plots adjacent to ungrazed plots could be observed in the Sönke-Nissen-Koog salt marsh, north of the Hamburger-Hallig area (Sieger 2004, Kiehl 2005). Our results indicate that large-scale land-use change does not only affect the vegetation of the respective areas directly but can also have strong effects on neighbouring areas, in which the management did not change. Without any land-use change, species density would have remained low under continuously high grazing pressure.

In the low salt marsh, species density increased both on grazed and ungrazed plots. Our results show that the dominance of the low-marsh species *Atriplex portulacoides* did not have any negative effect on species density in our study area up to now. This is in contrast to the findings of other authors who stated that *Atriplex portulacoides* is able to outcompete other species in ungrazed salt marshes (Bakker 1989, Bos et al. 2002). In our study area, the neglectance of the drainage system has probably led to reduced aeration of the clayey soils, which prevented the dominance of *Atriplex* because this species is negatively affected by soil water logging (Beeftink 1977).

In the high salt marsh, species density also increased on most plots but showed a slight and not significant decrease on plots ungrazed since 1992. On the latter plots, species density had been highest (eight species per 4 m²) of all plots in the beginning of the study because grazing-sensitive species were already present with few individuals then. As the species pool in salt marshes is generally small due to the extreme environmental conditions (Adam 1990), a further strong increase of species density could not be expected. Nevertheless, first tendencies of a slight decrease in species density could be observed between 1995 and 2004. For these plots, the decreasing evenness values indicate increasing dominance of single species. For all other plots, evenness values decrease mainly due to the increasing species density because the dominance index 1/D of Williams (1964) is divided by the number of species in order to calculate the evenness index $E_{1/D}$.

The analysis of the difference in species density between 1999 and 2004 showed that *Elymus athericus* was able to outcompete other species in our study area. This confirms the findings of Bos et al. (2002). *Festuca rubra*, in contrast, as another competitive high marsh species was less competitive in our study area. Large-scale dominance of this species was probably also hampered by soil water logging (c.f. Gray & Scott 1977).

In summary, our results indicate that species density might decrease in the future in ungrazed plots on well aerated soils of the high salt marsh dominated by *Elymus* spp. In the low salt marsh and in less drained parts of the high salt marsh, soil water-logging and low sedimentation rates (Schröder et al. 2002, Kiehl et al. 2003) may impede species dominance and consequentially prevent a decrease in species density.

Figure 3: Intensively grazed salt marsh in the beginning of the 1990ies (Photo: K. Kiehl).

Figure 4: Ungrazed salt marsh of the Hamburger Hallig in 2002 (Photo: M. Stock).

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