Biol Invasions (2021) 23:871–883
https://doi.org/10.1007/s10530-020-02408-0

ORIGINAL PAPER

Long-term invasion dynamics of *Spartina* increase vegetation diversity and geomorphological resistance of salt marshes against sea level rise

Dirk Granse · Sigrid Suchrow · Kai Jensen

Received: 7 June 2020 / Accepted: 28 October 2020 / Published online: 3 December 2020

Abstract The cordgrass *Spartina anglica* C.E. Hubbard (*Poaceae*) is an invasive transformer in many salt marsh ecosystems worldwide. Relatively little is known about the capacity of *Spartina* to accelerate salt marsh succession and to protect salt marshes against sea level rise. We analyzed long-term changes in vegetation and elevation in mainland salt marshes of the European Wadden Sea in Schleswig-Holstein, Germany, to estimate the impact of non-native *Spartina* on the geomorphological resistance of salt marshes to sea level rise and on changes in species diversity. From 1989 to 2019, the *Spartina*-zone shifted and expanded upwards to elevations of the high marsh zone and *Spartina* increased in frequency in several salt marsh vegetation communities. At sites where *Spartina* dominated the vegetation already three decades ago, elevation and species diversity increased with a higher rate compared to sites lacking *Spartina*. The median change rates reached for elevation MHT +8.6 versus +1.5 mm per year, for species richness +3 versus ±0 species per three decades, and for evenness +0.04 versus −0.08 per three decades, regarding plots with versus without former *Spartina* dominance, respectively. Invasion of salt marshes by *Spartina* and its continued, long-term presence were associated with increased elevation and species diversity in the face of sea level rise.

Keywords Accretion · Ecological amplitude · Ecosystem functioning · Elevational range · Species diversity · *Spartina* · *Sporobolus*

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02408-0) contains supplementary material, which is available to authorized users.

D. Granse (✉) · S. Suchrow · K. Jensen
Applied Plant Ecology, Institute of Plant Science and Microbiology, Universität Hamburg, Hamburg, Germany
e-mail: dirk.granse@uni-hamburg.de

Introduction

Introductions of non-native *Spartina anglica* C.E. Hubbard (common cordgrass) profoundly affect coastal ecosystems and their native species communities (e.g., Partridge 1987; Hedge and Kriwoken 2000; Hacker et al. 2001; Raybould 2005; Sheehan and Ellison 2014). *Spartina* × *anglica* is the genome-duplicated descendent of the F_1-hybrid *Spartina* × *townsendii* H. Groves & J. Groves which emerged from hybridization of *Spartina maritima* (Curtis) Fernald and *Spartina alterniflora* Loiseleur in the 19th century in Britain (Marchant 1967). These taxa belong to a monophyletic lineage of *Spartina* that was recently included in the genus *Sporobolus* (Peterson et al. 2014). *Spartina* × *townsendii* and *Spartina anglica*, in the following synonymously referred as *Spartina*, were valued for the capacity to catch and stabilize tidal sediments (Ranwell 1967) and therefore, they were introduced along coasts of several continents (Strong and Ayres 2013). As *Spartina* can change the character, condition, form, or nature of ecosystems over substantial areas by silting up tidal marshes and creating new habitat (cf. Lee and Partridge 1983; Strong and Ayres 2009; Simberloff 2011; Sheehan and Ellison 2014), it can be considered an invasive transformer according to the concept of Richardson et al. (2000).

The population development of introduced plant species in a non-native range is affected by many factors, such as genetic-diversity related propagule pressure, the capacity to reproduce by autogamy, and competition with native species (Facon et al. 2006). Population dynamics often show a time-lag between the original introduction and a subsequent sharp population increase (Facon et al. 2006; Richardson et al. 2010). Furthermore, native communities can show biotic resistance against successful establishment of non-natives (Elton 1958; Knops et al. 2002; Levine et al. 2004) whereas disturbances can play an important role in facilitating invasions (Davis et al. 2000; Richardson et al. 2000; Pyšek et al. 2010). Non-natives can also themselves cause changes in disturbance regimes and therefore alter the development of native communities which are under control of the respective disturbances (reviewed by Mack and D'Antonio 1998), e.g., by mitigating or enhancing effects of fire regimes (D'Antonio and Vitousek 1992; D'Antonio et al. 2017). However, impacts of non-natives on ecosystems can change over time and former invaded areas may again be 'released' after an initial establishment success (Blackburn et al. 2011). Thus, impact assessments of invasive species require long-term observations of their population dynamics and their interactions with native plants (cf. Osborne and Gioria 2018; Stricker et al. 2015). In this study, we use data from long-term vegetation monitoring to investigate the invasion dynamics of *Spartina* in Wadden Sea salt marshes.

Spartina was introduced into the European Wadden Sea area in the 1920s on purpose for coastal protection and land reclamation (e.g., König 1948; Esselink and Essink 1998). Since the second half of the last century, a continuous expansion of *Spartina* has been recorded in Wadden Sea salt marshes (Nehring and Hesse 2008; Esselink et al. 2009, 2017). *Spartina*-stands can, however, also exhibit considerable die-backs (König 1948; Goodman et al. 1959; Raybould 2005). Moreover, *Spartina*-swards can be colonized by other salt marsh species during succession (particularly by *Puccinellia maritima*; Scholten and Rozema 1990; Gray et al. 1991). Gray et al. (1991) argued that *Spartina* has the capacity to facilitate the establishment of native plant species by protecting them from uprooting by water current forces.

Three decades ago, *Spartina* was mostly observed on elevations below mean high tide (MHT) in the Wadden Sea area (cf. Suchrow and Jensen 2010). More recent observations indicate that the upper boundary of the *Spartina*-zone shifted towards the mean high tide spring (MHT_{spring}) elevation mark (cf. Gray et al. 1991; Daehler and Strong 1996; Raybould 2005, pers. observation). In areas above MHT, substantial changes in abiotic conditions (e.g., Adam 1993) and associated changes in vegetation occur. Areas above the MHT_{spring} elevation mark are usually regarded as high marsh communities. *Spartina* is supposed to be excluded from these higher elevations by competition from native vegetation (Scholten and Rozema 1990; Gray et al. 1991; Gray and Mogg 2010). Relatively little is known about the invasion dynamics of non-native *Spartina* in native vegetation communities on elevations above MHT.

Wadden Sea salt marshes of the mainland coast of Germany, Denmark and the Netherlands are mostly 'man-made' habitats which resulted from land reclamation activities over centuries. In front of sea walls, rectangular sedimentation fields protected by brushwood groynes were created on intertidal flats. In addition, ditches were dug out to increase drainage of the developing salt marshes. Traditionally, the developing salt marshes have been used for livestock grazing (mainly cattle and sheep). After the establishment of National Parks in the German Wadden Sea in the late 1980s, land-use management of salt marshes has been changed widely. In large areas, the maintenance of the artificial drainage system ceased and livestock grazing was abandoned (Stock et al. 2005). Changes in grazing represent a fundamental shift in the disturbance regime of the Wadden Sea salt marshes. In addition, changes in the flooding regime due to sea level rise (cf. Schuerch et al. 2013; Oost et al. 2017) act as a hydrologic stressor on salt marsh vegetation.

The objectives of this study are to investigate long-term invasion dynamics of non-native *Spartina* and its impacts on native species communities and on ecosystem functioning in Wadden Sea salt marshes. We aim to understand how the invasion dynamics are affected by changes in the disturbance regime and whether *Spartina* may mitigate increasing hydrologic stress of the salt marshes by increasing accretion rates. We used vegetation and elevation data on 1 m^2 scale from three decades ago and from a recent resampling to evaluate the following hypotheses:

1. The *Spartina*-zone expanded to the MHT_{spring} elevation mark. This was tested by means of niche-models regarding the response of *Spartina* to the elevational gradient and tidal data.
2. *Spartina* increased in frequency in native salt marsh communities. The species benefitted from the abandonment of livestock grazing. To test this, we compared the recent frequency of *Spartina* in salt marsh communities with the frequency three decades ago considering different grazing regimes as a predictor of disturbance.
3. *Spartina* mitigates negative effects of sea level rise in salt marshes by increasing accretion. Positive effects of *Spartina* on ecosystem functioning are also represented by higher species diversity. This hypothesis was tested by comparing elevation changes and changes in species diversity of salt marshes with and without the presence of *Spartina*.

Methods

Study area and sampling

The study was carried out in mainland salt marshes along the coastline of the Wadden Sea of Schleswig-Holstein, Germany (Fig. 1). Data collection of this study (referred as 2019) is based on a resampling of plots investigated by Suchrow and Jensen (2010) three decades ago (referred as 1989). The study area was split up in six regions reflecting comparable tidal regimes as proposed by Balke et al. (2016). The salt marshes in the study area were intensively grazed (usually by sheep) until the 1980s. Then, grazing was abandoned in parts of the study area and maintained in others.

Transect investigation

To analyze the invasion dynamics of *Spartina*, we resampled 362 plots (1×1 m^2) along 19 out of 121 transects originally installed in 1989 (Suchrow and Jensen 2010). The 19 transects were chosen to a) have representative numbers of plots in each of the six regions and b) cover both grazed and ungrazed salt marshes. To account for marsh areas that developed since the first inventory in 1989, transects were elongated downwards the elevational gradient by adding further 667 plots with vegetation. These plots also covered the most seawards located vegetation in patches of *Salicornia* spp. and *Spartina*. To enable niche-modeling with respect to the elevational gradient from tidal flat to high marsh zone, additional 93 plots were placed in unvegetated parts nearby vegetated plots on the tidal flats. The final data set comprised 1122 plots.

Field work was carried out during the growing seasons, from July to October in 2017, 2018, and 2019, respectively. On all plots, GPS coordinates were recorded and percent rooted cover (cf. Dengler et al. 2016) was estimated for each species as well as total vegetation cover. If identification beyond the genus was not possible in the field (e.g. for *Salicornia*), the cover was aggregated on group level. Hereafter, all taxa are referred as 'species'. The data on species composition is available in the collaborative vegetation-plot database 'GrassPlot' (see Dengler et al. 2018). For each plot with a total vegetation cover of $\geq$10%, the vegetation was assigned to a salt marsh community with respect to vegetation cover and species' dominance (cf. van Bernem et al. 1994). The proportion of plots harboring *Spartina* is reported as frequency of *Spartina* in communities (for a list of communities see Online Resource, Table 1). Species nomenclature follows Wisskirchen et al. (1998).

Changes in species richness (species number per plot) and evenness were used as indicators for the impact of *Spartina* on the diversity of native plant species. Evenness was calculated following Pielou (1966) and Haeupler (1982), allowing for direct comparison of the dominance structure even if plots have different species numbers.

The status of *Spartina* on each of the plots was categorized to be 'stable' (present in 1989 and 2019), 'disappeared' (present in 1989 but absent in 2019), 'established' (not present in 1989 but recorded in

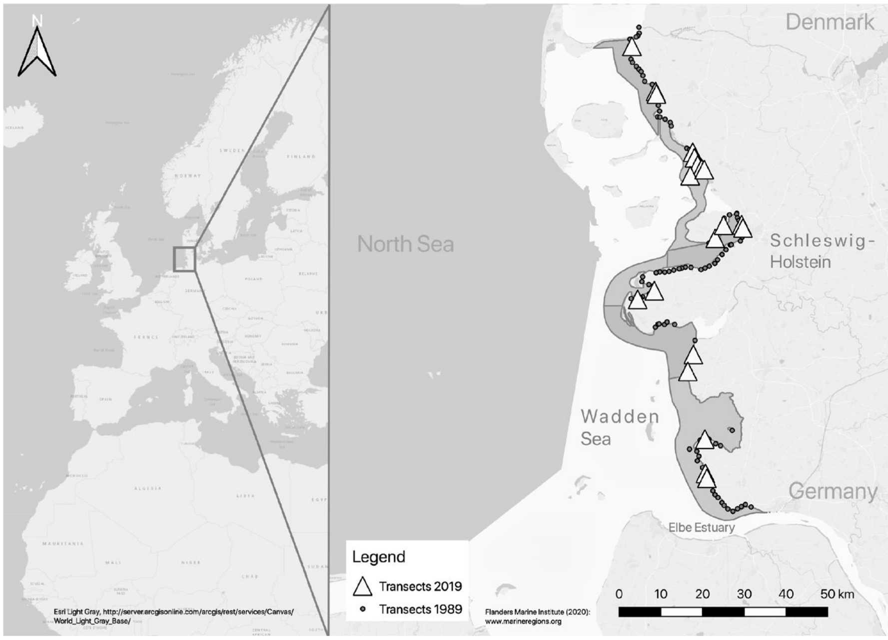

Fig. 1 Study area of mainland salt marshes in the European Wadden Sea along the North Sea coast of Schleswig-Holstein, Germany. The accentuated areas along the coast represent six regions with comparable tidal regimes. The position of transects is displayed by black dots (1989) and white triangles (2019)

2019) and 'absent' (neither observed in 1989 nor in 2019).

To account for grazing management (categories: ungrazed, grazed; see Online Resource, Table 2), the GPS positions of the plots were intersected with the GIS-shapes containing data on salt marsh management from the Common Trilateral Monitoring and Assessment Programme (TMAP; surveys 1980 to 2016; cf. Petersen et al. 2014; Esselink et al. 2017).

Elevation and tidal data

Elevation of plots above sea level in 1989 was taken from the survey of Suchrow and Jensen (2010). In 2019, elevation was measured again, either in relation to benchmarks of the vertical control survey net (see Suchrow and Jensen 2010) or to sedimentation erosion bars (see Stock 2011). Leveling was done optically using a Spectra Precision Laser Level LL500 (by Trimble) in combination with a rod mounted HL700 receiver (accuracy 0.5 mm). The measured values were related to NN (German ordnance level) resulting in absolute elevation values.

Mean high tide (MHT) data were obtained from automatically recording tide gauges along the coast (data for 'previous water-year', provided by the National Park authorities). In regions with one gauge available, the MHT value of a gauge was directly assigned to a transect, whereas in regions with two gauges available, the MHT value was interpolated with respect to the geographical position of a transect between gauges. The transect's MHT value was used to convert the plot's absolute elevation (related to NN) into a corresponding elevation in relation to MHT. This allows to compare plot elevations, adjusted against accretion and sea level rise, and independent of regional differences in tidal range. The MHT_{spring} elevation was assumed to be 35 cm above MHT (see Wanner et al. 2014).

Niche-modeling

Niche-models were created by calculating responses of *Spartina* in relation to the elevational gradient in 1989 and 2019, respectively. For this, presence-absence-data (frequency limit 1%) was related to elevation MHT values applying HOF-modeling (Huisman-Olff-Fresco-models; Huisman et al. 1993) using the R-package eHOF (Jansen and Oksanen 2013) with default settings. Model runs were bootstrapped 100 times, and the best-fitting model was determined using AICc (Akaikes information criterion; cf. Burnham and Anderson 2004). The HOF-model parameter and niche-parameter predictions are listed in Online Resource, Tables 3–5. For unimodal HOF-models, the niche-optimum is defined as the elevation with the maximal predicted probability of occurrence and the central niche-boundaries were calculated as the range where the response decreases to 0.6 times the height of the maximal response (Jansen and Oksanen 2013). The calculated central niche-boundaries corresponded approximately with the range of *Spartina*'s main occurrence. A response-decrease to 0.5 times the niche-optimum was used to define the upper boundary of the *Spartina*-zone. We assumed that the predicted upper boundary coincides with the MHT_{spring} elevation and we used +35 cm MHT as elevation mark to separate the *Spartina*-zone from the high marsh zone. To compare predicted versus observed frequencies of *Spartina*, the recorded cover values of *Spartina* were transformed into a binary presence/absence-status (presence: cover $>$ 0; absence: cover = 0). The observed frequency was calculated as meanvalue from presence/absence-status over binning classes of 10 cm MHT of elevation.

Software and statistics

Geographic data was analyzed using QGIS (3.4.11-Madeira) with HCMGIS-plugin (including Esri World Light Grey Basemap) and Marine Regions shape file (Flanders Marine Institute, 2020). All statistical analyses were conducted within the computing environment R (version 3.6.1; R Development Core Team, 2011).

The normality of the data was tested using a Shapiro-Wilk test by applying the R-function shapiro.test() on the residuals from ANOVA analysis results. The homogeneity of variance across groups was computed by means of Levene's test (leveneTest). The data of the multifactorial responses (i.e., frequency of *Spartina* in vegetation communities as well as changes in elevation, species richness, and evenness; see below) was either not normally distributed (although Box-Cox transformed), or did not meet condition of variance homogeneity, or showed high variation in *n* between categorical groups of the regarded factors. Therefore, the multifactorial data was evaluated by means of non-parametric Kruskal-Wallis tests by testing all combinations of categorical groups of the considered factors against each other. Kruskal-Wallis tests were followed by post-hoc multiple pairwise Mann-Whitney *U* tests with Bonferroni-Holm adjusted *P*-values. The letter-codes illustrating significant differences between evaluated factorial categories were generated from the results of the Mann-Whitney *U* tests using R-function multcompLetters() from the R-package multcompView (Piepho 2004).

Evenness was calculated using the function diversity() from the R-package vegan with option 'shannon' and normalizing the results through division with log(species richness), on condition that species richness was higher than one.

Differences in the frequency of *Spartina* in vegetation communities were evaluated using a ($2 \times 2 \times 2$) factorial test design as follows: frequency $\sim$ marsh-zone (*Spartina*-zone, high marsh) + management (ungrazed, grazed) + year (1989, 2019).

Changes in elevation (and also in species richness and evenness; see Online Resource, Tables 6–8) were compared within a (2×2) factorial test design. Due to unbalanced categorical groups (*Spartina*-status), a non-parametric Kruskal-Wallis test was used by evaluating categorical groups of all factorial combinations as follows: response $\sim$ *Spartina*-status (absent, disappeared, established, stable) + *Spartina*-dominance in 1989 (*Spa* vegetation community, other vegetation community).

Changes in species richness and evenness were evaluated with respect to the marsh zone and *Spartina*-dominance in a (2×2) factorial design as follows: response $\sim$ marsh-zone (*Spartina*-zone, high marsh) + *Spartina*-dominance in 1989 (*Spa* vegetation community, other vegetation community).

Results

Spartina-response to the elevational gradient

The niche-models of the response of *Spartina* to the elevational gradient in relation to MHT showed a unimodal shape, with increased skewness towards higher elevations in 2019 (Fig. 2). The niche-optimum shifted by over 50 cm from −46.4 cm MHT in 1989 to 4.9 cm MHT in 2019. The response curve of 2019

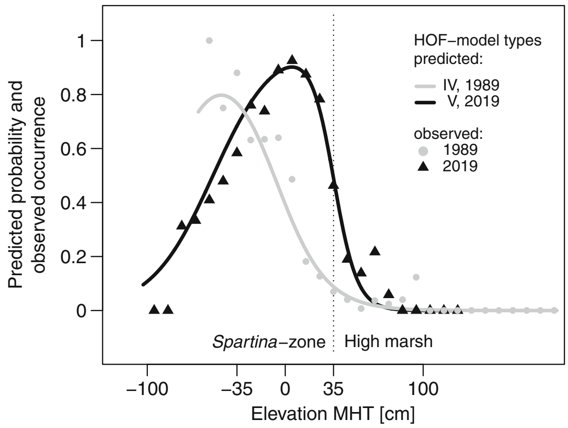

Fig. 2 HOF-calculated niche-models based upon the presence/absence of *Spartina* along the elevational (MHT) gradient for data from 1989 (2691 plots) to 2019 (1122 plots). The points and triangles show the mean frequency of *Spartina*-presence in binning classes of 10 cm along the elevational gradient, indicating the model's goodness of fit. The perpendicular dotted line indicates the assumed MHT_{spring} elevation mark (according to Wanner et al. 2014)

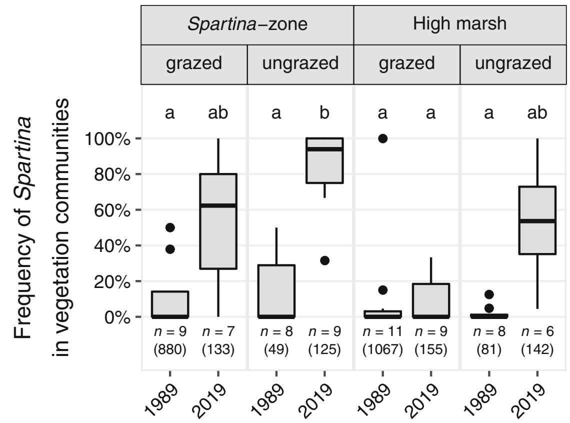

Fig. 3 Frequency of *Spartina* in vegetation communities in relation to marsh-zone (*Spartina*-zone, high marsh), salt marsh management (grazed, ungrazed), and year of vegetation assessment (1989, 2019). The letter-codes (a, b) indicate pairwise differences in *Spartina*'s frequency between years, salt marsh management, and marsh zones; Kruskal-Wallis test followed by Mann-Whitney *U* tests with Bonferroni-Holm adjustment, $H = 32.4, P < 0.05, df = 7, n =$ salt marsh communities (excluding *Spa* vegetation community; number of plots in brackets). In the boxplots, the median is displayed as horizontal line and outliers as dots outside the 1.5 of the interquartile range (box and whiskers)

decreased steeper at higher elevations than the curve of 1989. At 35 cm MHT, the probability of occurrence was predicted to be half of the niche-optimum in 2019, coinciding with the assumed MHT_{spring} elevation. In 1989, the central niche ranged from −63.0 to −6.9 cm MHT. Until 2019, the central niche shifted and expanded towards −48.1 to 33.0 cm MHT. The observed frequency of occurrence of *Spartina* in 2019 scattered relatively tightly along the predicted response curve of 2019. Niche-optimum and rawmean differed only slightly by 8.6 cm. Both, relatively high similarity in predicted versus observed data as well as in niche-optimum versus raw mean, pointed to a good agreement on the model-prediction in 2019 (see also detailed HOF-model diagrams in Online Resource Fig. 7 and predicted HOF-model responses in Online Resource, Table 3).

Frequency of *Spartina* in different salt marsh communities

The frequency of *Spartina* increased from 1989 to 2019 in main salt marsh communities of the *Spartina*-zone, particularly on ungrazed plots (Fig. 3; frequency of *Spartina* in selected salt marsh communities see Online Resource, Fig. 8). In contrast to the *Spartina*-zone, the frequency of *Spartina* did not increase from 1989 to 2019 under grazing in the high marsh zone. In ungrazed conditions of the high marsh, however, *Spartina* (non-significantly) increased in frequency between 1989 and 2019.

Spartina and ecosystem functioning: elevation change and species diversity

Elevation change between 1989 and 2019 was highest on plots with *Spartina*-dominance in 1989 and if *Spartina* was considered stable until 2019 (Fig. 4). On average, these plots were located few centimeters above MHT in 2019. Compared to these *Spartina*-dominated plots, the elevation change was generally lower on plots without *Spartina*-dominance in 1989, particularly if *Spartina*-vegetation remained stable, did establish, or stayed absent. Independent of whether or not *Spartina* was the dominant species in 1989, plots where *Spartina* disappeared showed relatively high elevation change rates on high marsh elevations.

Species richness increased from 1989 to 2019 with the highest rates if *Spartina* was already dominating on plots in 1989 (Fig. 5). Particularly high increases were observed in the *Spartina*-zone under *Spartina*-dominance. Opposed to this, species richness decreased in the high marsh zone if *Spartina* was not the dominant plant species in 1989. In addition, the evenness change rate increased little from 1989 to 2019 in the *Spartina*-zone if *Spartina* was dominant in 1989 (Fig. 6). This was different for plots on high marsh elevations where the evenness decreased on plots independently of former *Spartina*-dominance.

Discussion

The niche-models of *Spartina* from 1989 and 2019 indicate a shift of the central niche-range towards higher elevations and thus support our first hypothesis that the *Spartina*-zone expanded to the MHT_{spring} elevation mark. Indeed, between 1989 and 2019, the *Spartina*-zone shifted and expanded up to the MHT_{spring} elevation mark. Above this elevation mark, *Spartina* was widely excluded from the high marsh habitats. This is most likely due to competitive displacement of *Spartina* by other species (cf. Scholten et al. 1987; Scholten and Rozema 1990; Gray et al. 1991). Accordingly, the MHT_{spring} elevation mark has previously been shown to be linked with changes in species composition due to alleviated abiotic stress with lower flooding frequencies (Adam 1993;

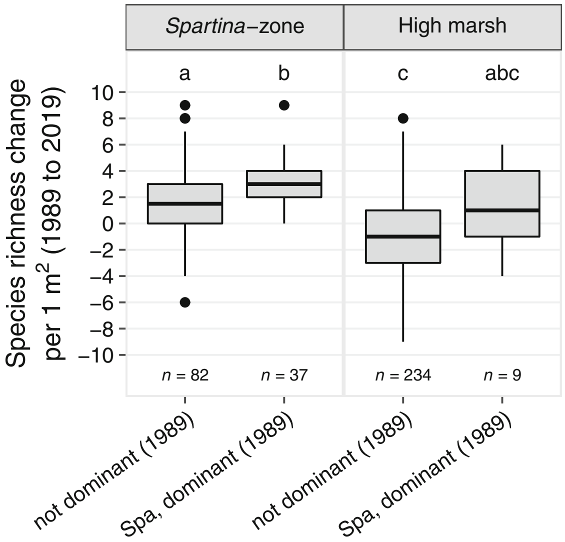

Fig. 5 Changes in species richness from 1989 to 2019 in relation to *Spartina*-dominance (*Spa* vegetation community in 1989: not dominant, *Spa* dominant), separately for the marsh zones (*Spartina*-zone, high marsh) in 2019. The letter-codes (a, b, c) indicate pairwise differences in species richness change between *Spartina* dominance types and marsh zones; Kruskal-Wallis test followed by pairwise Mann-Whitney *U* tests and Bonferroni-Holm adjustment, $P < 0.05$, $df = 5$, $n = 362$ plots). For detailed statistic values see Online Resource, Table 7. In the boxplots, the median is displayed as horizontal line and outliers as dots outside the 1.5 of the interquartile range (box and whiskers)

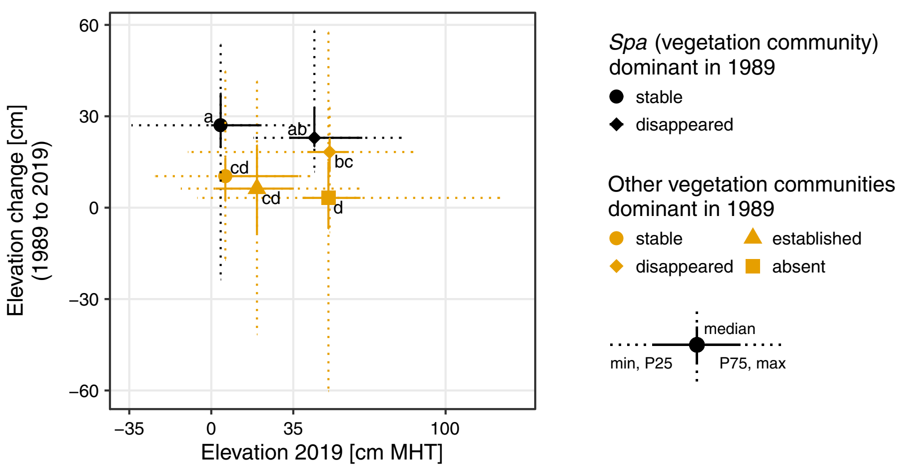

Fig. 4 Changes in elevation MHT from 1989 to 2019 in relation to *Spartina*-dominance (*Spa* vegetation community dominant, other vegetation community dominant) in 1989 and to *Spartina*-status (stable, established, disappeared, absent) in 2019. The letter-codes (a, b, c, d) indicate pairwise differences in elevation change between *Spartina* dominance types and *Spartina*-status; Kruskal-Wallis test followed by pairwise Mann-Whitney *U* tests and Bonferroni-Holm adjustment, $P < 0.05$, $df = 5$, $n = 362$ plots). For detailed statistic values see Online Resource, Table 6

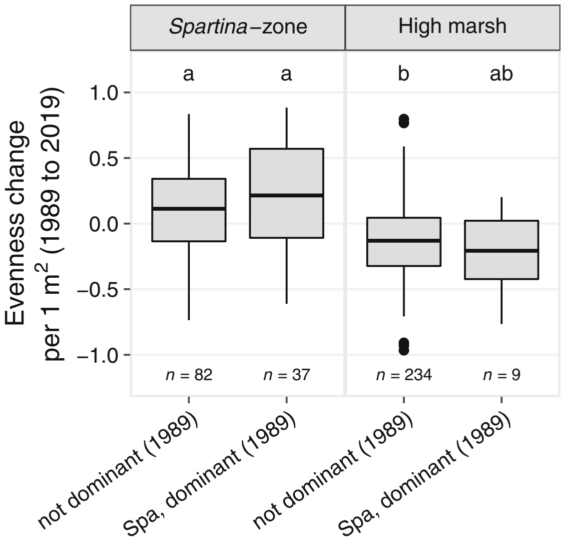

Fig. 6 Changes in evenness from 1989 to 2019 in relation to *Spartina*-dominance (*Spa* vegetation community in 1989: not dominant, *Spa* dominant), separately for the marsh zones (*Spartina*-zone, high marsh) in 2019. The letter-codes (a, b) indicate pairwise differences in evenness change between *Spartina* dominance types and marsh zones; Kruskal-Wallis test followed by pairwise Mann-Whitney *U* tests and Bonferroni-Holm adjustment, $P < 0.05$, $df = 5$, $n = 362$ plots). For detailed statistic values see Online Resource, Table 8. In the boxplots, the median is displayed as horizontal line and outliers as dots outside the 1.5 of the interquartile range (box and whiskers)

Amsberry et al. 2000; Suchrow and Jensen 2010). Today, the *Spartina*-zone and the high marsh zone can be considered as contiguous marsh zones, separated from each other near the MHT_{spring} elevation mark.

Spartina has increased in frequency between 1989 and 2019, especially in ungrazed salt marshes. Today, it is found more often in several native salt marsh communities than three decades ago. This observation supports our second hypothesis that *Spartina* increased in frequency in native salt marsh communities and benefitted from the abandonment of livestock grazing. After abandonment of grazing, *Puccinellia maritima* dominated vegetation developed widely into *Atriplex portulacoides* dominated vegetation in low marshes (Jensen 1985; Stock et al. 1998; Bakker et al. 2003). In higher elevated areas without grazing, *Festuca rubra* communities widely decreased and the *Elymus athericus* community became dominant (Bakker et al. 2003; Wanner et al. 2014; Bakker et al. 2020). According to our findings, *Spartina* benefitted from changes in the disturbance regime, i.e., the abandonment of grazing. Under ungrazed conditions, vegetation communities dominated by grazing tolerant species, such as *Puccinellia maritima* and *Festuca rubra*, were more often invaded by *Spartina* than under grazing.

Grazing can exert direct and indirect effects on the performance of non-native species (Petruzzella et al. 2020). Direct effects address the reduction of non-native's biomass or their damage by trampling, while indirect effects address shifts in biotic interactions between native and non-native plant species and associated herbivores. Sheep usually show selective feeding (Jensen 1985) and do not prefer *Spartina* (Ranwell 1961). Trampling damage by livestock grazers (cf. Nolte et al. 2015) and shifts in the competitive interactions with other species (cf. Bando 2006; Petruzzella et al. 2020) seem to be likely reasons for a suppression of *Spartina* under grazed conditions. In ungrazed areas, both the release from trampling damage and a competitive advantage over grazing tolerant species may have led to an increase of non-native *Spartina*.

During the last three decades, increased change rates in elevation relative to MHT were associated with a former dominance of *Spartina*. This observation supports the first part of our third hypothesis that *Spartina* mitigates negative effects of sea level rise in salt marshes by increasing accretion. Particularly, the resampled plots with a former dominance of *Spartina* showed accelerated positive accretion. Positive accretion in a sufficient range is a critical requirement to keep salt marsh elevation in equilibrium with sea level rise (e.g., Fagherazzi et al. 2012; Kirwan and Megonigal 2013; Schuerch et al. 2013, 2014). After three decades of development, the plots with former *Spartina* dominance had also changed in vegetation communities but were still harboring *Spartina*. With increasing plot elevation, initial dominance of non-native *Spartina* decreased under competition by colonizing natives (cf. Engels et al. 2011; Proença et al. 2019; Petruzzella et al. 2020). This observation is in line with results of Flory et al. (2017) who showed that an initially abundant non-native annual grass was successionally suppressed by native vegetation.

In salt marsh areas with decreasing elevation (e.g., due to compaction, cf. Bartholdy et al. 2010; Nolte et al. 2013), stands of native species can get lost if these species fail to persist under increasingly severe abiotic conditions (Thompson 1991). In these areas, *Spartina* can act as fill-in species (cf. Ranwell 1967; Proença et al. 2019) by establishing in old ditches of the abandoned drainage system (cf. Hartmann and Stock 2019) or in habitats getting vacant due to negative accretion and rewetting (cf. Stock 2011). The latter is well reflected by our data regarding plots where *Spartina* established after 1989, mostly in the elevational range between MHT and high marsh zone (see Fig. 4). These plots showed comparatively low or negative elevation change rates, which points to salt marsh compaction and high geomorphological dynamics. At the same time, a comparatively high species diversity indicates that native vegetation communities were already well established on plots with new *Spartina*-establishment (see Online Resource, Fig. 9). *Spartina* may mitigate compaction and sea level rise effects by means of increasing accretion rates after establishment.

In the present study, *Spartina*-patches were regularly found at the seaward end of the salt marshes, indicating that this species played a role in extending salt marshes into low-elevated tidal flats. However, the spread of *Spartina* into relatively low-elevated areas was limited, presumably due to constrictions imposed by flooding regimes (Gray et al. 1990), wave energy (Widdows et al. 2008) or a vanishing window of opportunity for seedling establishment (Balke et al. 2016). Nevertheless, *Spartina*-patches with a tussock shape are known to be involved in pioneer zone development (Balke et al. 2012; Sheehan and Ellison 2014), but this process is limited at too low elevations (Hubbard 1969; Lee and Partridge 1983). Ladd et al. (2019) showed that sediment availability is more important for the extension of salt marshes in Great Britain than the presence of *Spartina*. We infer that *Spartina* initiates salt marsh development above a certain threshold elevation, in our study approximately -35 cm MHT.

Species richness of salt marsh communities increased over the last three decades with higher rates and evenness change was highest if non-native *Spartina* was formerly the dominant species. This supports the second part of our third hypothesis that positive effects of *Spartina* on ecosystem functioning in Wadden Sea salt marshes are also represented by higher species diversity. This seems to contradict the notion that *Spartina* replaces more diverse native plant communities (e.g., Doody 1990; Nehring and Hesse 2008). The capacity of *Spartina* for engineering coastal ecosystems has been known already. Beyond that, *Spartina*'s capacity for ecosystem engineering may have also led to increased habitat complexity and species diversity (Crooks 2002; Hacker and Dethier 2006).

Despite of positive effects of *Spartina* on diversity, we want to acknowledge, however, that also other factors may have contributed to a higher diversity. In salt marshes, species richness generally increases with elevation (Suchrow et al. 2015). Another important factor for increasing species diversity may be the abandonment of livestock grazing of Wadden Sea salt marshes in the late 1980s (Kiehl et al. 2003, 2007; Wanner et al. 2014). The species diversity in Wadden Sea salt marshes increased after this pronounced change in management even in areas with a continuous high-density grazing. It has been argued that increasing seed availability of successfully reproducing grazing-sensitive species growing in moderately grazed or ungrazed salt marshes in the vicinity may have contributed to this effect (Kiehl et al. 2007).

After the successful establishment of non-native species, micro-evolution may lead to the adaptation of native species to the novel community dominated by a non-native (cf. Leger and Goergen 2017). This may increase the capacity for species coexistence (cf. D'Antonio and Flory 2017). In addition, new ecotypes in native species may evolve over time, as e.g., in *Elymus athericus* (Bockelmann et al. 2003) or in *Puccinellia maritima* (Rouger and Jump 2015). If these new ecotypes exhibit a shift in their niche-range compared to their putative ancestors, these ecotypes may potentially share niche-ranges with non-natives and thereby increase diversity. Our data suggest that long-term presence of non-native *Spartina* has not been accompanied by a decrease in species diversity of native vegetation.

Conclusions

In European Wadden Sea salt marshes, non-native *Spartina* can be considered an invasive transformer whose impacts extend far beyond effects of initial ecosystem engineering during its establishment. Today, *Spartina* is co-occurring in several native salt marsh communities. *Spartina* showed its highest (positive) effect on species diversity and accretion rates if it was the dominant species during early stages of salt marsh development. By accelerating accretion rates on the long run, *Spartina* stabilizes not only salt marsh elevation relative to sea level rise, but also provides habitat for native species. However, the occurrence and therefore effects of *Spartina* were mainly limited to elevations of the *Spartina*-zone below MHT_{spring}. Further research is needed to investigate whether these effects are limited to the Wadden Sea salt marshes or whether they also occur during *Spartina*-invasions in other parts of the world.

Acknowledgements We would like to thank the authorities from the Nationalpark Schleswig-Holsteinisches Wattenmeer for the authorization of our fieldwork, providing TMAP vegetation data (Trilateral Monitoring and Assessment Programme; https://www.waddensea-secretariat.org), and tidal data. We further would like to thank the Wasserstraßen- und Schifffahrtsamt Tönning, Landesbetrieb für Küstenschutz und Nationalpark und Meeresschutz for providing tide gauge measurements. All work was conducted in the framework of the project 'Hybrids - Chances and Challenges of New Genetic Combinations', Universität Hamburg, funded by the state of Hamburg, Germany. We also thank the anonymous reviewers for their constructive and helpful suggestions.

Author contributions All authors contributed to the study conception and design. Vegetation assessments in 1989 were performed by Sigrid Suchrow. Vegetation assessments in 2019 and data compilation were performed by Sigrid Suchrow and Dirk Granse. The data analysis was performed and the first draft of the manuscript was written by Dirk Granse (however, the methods-section in equal parts by Sigrid Suchrow and Dirk Granse). Kai Jensen contributed extensive wording to the final version of the manuscript. All authors commented on previous versions of the manuscript and all authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Adam P (1993) Saltmarsh ecology. Cambridge University Press, Cambridge

Amsberry L, Baker MA, Ewanchuk PJ, Bertness MD (2000) Clonal integration and the expansion of phragmites Australis. Ecol Appl 10(4):1110–1118. https://doi.org/10.1890/1051-0761(2000)010[1110:CIATEO]2.0.CO;2

Bakker JP, Bos D, De Vries Y (2003) To graze or not to graze: that is the question. In: Proceedings of the 10th International Scientific Wadden Sea Symposium, vol 67, p 88

Bakker JP, Schrama M, Esselink P, Daniels P, Bhola N, Nolte S, de Vries Y, Veeneklaas RM, Stock M (2020) Long-term effects of sheep grazing in various densities on marsh properties and vegetation dynamics in two different salt-marsh zones. Estuaries Coasts 43(2):298–315. https://doi.org/10.1007/s12237-019-00680-5

Balke T, Klaassen PC, Garbutt A, van der Wal D, Herman PMJ, Bouma TJ (2012) Conditional outcome of ecosystem engineering: a case study on tussocks of the salt marsh pioneer Spartina anglica. Geomorphology 153–154:232–238. https://doi.org/10.1016/j.geomorph.2012.03.002

Balke T, Stock M, Jensen K, Bouma TJ, Kleyer M (2016) A global analysis of the seaward saltmarsh extent: the importance of tidal range. Water Res Res. https://doi.org/10.1002/2015WR018318

Bando KJ (2006) The roles of competition and disturbance in a marine invasion. Biol Invasions 8(4):755–763. https://doi.org/10.1007/s10530-005-3543-4

Bartholdy J, Pedersen JBT, Bartholdy AT (2010) Autocompaction of shallow silty salt marsh clay. Sediment Geol 223(3–4):310–319. https://doi.org/10.1016/j.sedgeo.2009.11.016

Blackburn T, Pyšek P, Bacher S, Carlton J, Duncan R, Jarošík V, Wilson J, Richardson D (2011) A proposed unified framework for biological invasions. Trends Ecology Evol 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bockelmann AC, Reusch TBH, Bijlsma R, Bakker JP (2003) Habitat differentiation versus isolation-by-distance: the genetic population structure of Elymus athericus in European salt marshes. Mol Ecol 12(2):505–515. https://doi.org/10.1046/j.1365-294X.2003.01706.x

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33(2):261–304. https://doi.org/10.1177/0049124104268644

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97(2):153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Daehler CC, Strong DR (1996) Status, prediction and prevention of introduced cordgrass Spartina spp. invasions in Pacific estuaries, USA. Biol Conserv 78(1):51–58. https://doi.org/10.1016/0006-3207(96)00017-1

D'Antonio C, Flory SL (2017) Long-term dynamics and impacts of plant invasions. J Ecol 105(6):1459–1461. https://doi.org/10.1111/1365-2745.12879

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23(1):63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

D'Antonio CM, Yelenik SG, Mack MC (2017) Ecosystem versus community recovery 25 years after grass invasions and fire in a subtropical woodland. J Ecol 105(6):1462–1474. https://doi.org/10.1111/1365-2745.12855

Davis M, Grime J, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–536. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dengler J, Boch S, Filibeck G, Chiarucci A, Dembicz I, Guarino R, Henneberg B, Janišová M, Marcenò C, Naqinezhad A, Polchaninova NY, Vassilev K, Biurrun I (2016) Assessing plant diversity and composition in grasslands across spatial scales : the standardised EDGG sampling methodology. Bullettin of the Eurasian Dry Grassland Group 32:13–30, https://eref.uni-bayreuth.de/41339/

Dengler J, Wagner V, Dembicz I, García-Mijangos I, Naqinezhad A, Boch S, Chiarucci A, Conradi T, Goffredo F, Guraino R, Janišová Monika, Steinbauer MJ, Aćić S, Acosta AT, Akasaka M, Allers MA, Apostolova I, Axmanová I, Bakan B, Baranova A, Bardy-Durchhalter M, Bartha S, Baumann E, Becker T, Becker U, Belonovskaya E, Bengtsson K, Benito Alonso JL, Berastegi A, Bergamini A, Bonini I, Bruun HH, Budzhak V, Bueno A, Campos JA (2018) GrassPlot-a database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48(3):331–347. https://doi.org/10.1127/phyto/2018/0267

Doody JP (1990) Spartina - friend or foe? A conservation viewpoint. In: Gray AJ, Benham PEM (eds) SPARTINA ANGLICA - a research review, chap 13, pp 77–79

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Engels JG, Rink F, Jensen K (2011) Stress tolerance and biotic interactions determine plant zonation patterns in estuarine marshes during seedling emergence and early establishment. J Ecol 99(1):277–287. https://doi.org/10.1111/j.1365-2745.2010.01745.x

Esselink P, Essink K (1998) Het Ems-Dollard estuarium. Ministerie van Verkeer en Waterstaat

Esselink P, Petersen J, Arens S, JP B, Bunje J, Dijkema K, Hecker N, Hellwig U, Jensen AV, Kers A, Körber P, Lammerts E, Stock M, Veeneklaas R, Vreeken M, Wolters M (2009) Salt Marshes. Thematic Report No. 8. Wadden Sea Ecosystem No 25 Quality Status Report 2009 Thematic Report No 8 46(4):27–30, http://www.waddensea-secretariat.org/sites/default/files/downloads/08-saltmarshes-10-09-21_0.pdf

Esselink P, Van Duin WE, Bunje J, Cremer J, Folmer EO, Frikke J, Glahn M, De Groot AV, Hecker N, Hellwig U, Jensen K, Körber P, Petersen J, Stock M (2017) Salt marshes. Tech. rep., Common Wadden Sea Secretariat, Wilhelmshaven, Germany. Last updated 21.12.2017. Downloaded 25.12.2017. qsr.waddensea-worldheritage.org/reports/salt-marshes, https://qsr.waddensea-worldheritage.org/reports/salt-marshes

Facon B, Genton BJ, Shykoff J, Jarne P, Estoup A, David P (2006) A general eco-evolutionary framework for understanding bioinvasions. Trends Ecol Evol 21(3):130–135. https://doi.org/10.1016/j.tree.2005.10.012

Fagherazzi S, Kirwan ML, Mudd SM, Guntenspergen GR, Temmerman S, D'Alpaos A, van de Koppel J, Rybczyk JM, Reyes E, Craft C, Clough J (2012) Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. Rev Geophys. https://doi.org/10.1029/2011RG000359

Flanders Marine Institute (2020) Marineregions.org. available online at www.marineregions.org. consulted on 2020-04-30. http://www.marineregions.org

Flory SL, Bauer J, Phillips RP, Clay K (2017) Effects of a non-native grass invasion decline over time. J Ecol 105(6):1475–1484. https://doi.org/10.1111/1365-2745.12850

Goodman PJ, Braybrooks EM, Lambert JM (1959) Investigations into 'Die-Back' in Spartina Townsendii AGG.: I. the present status of spartina townsendii in britain. J Ecol 47(3):651–677. https://doi.org/10.2307/2257297

Gray A, Mogg R (2010) Will Spartina anglica Invade Northwards With Changing Climate? In: Kerr DW, Ayres DR, Ericson SD, Olofson PR (eds) Proceedings of the Third International Conference on Invasive Spartina, pp 103–107

Gray AJ, Benham PEM, Raybould AF (1990) Spartina anglica - the evolutionary and ecological background. In: Gray AJ, Benham PEM (eds) Spartina anglica - a research review, London, HMSO, ITE research publication no. 2 edn, chap 1, pp 5–10

Gray AJ, Marshall DF, Raybould AF (1991) A century of evolution in Spartina anglica. Adv Ecol Res 21:1–62. https://doi.org/10.1016/S0065-2504(08)60096-3

Hacker SD, Dethier MN (2006) Community modification by a grass invader has differing impacts for marine habitats. Oikos 113(2):279–286. https://doi.org/10.1111/j.2006.0030-1299.14436.x

Hacker SD, Heimer D, Hellquist CE, Reeder TG, Reeves B, Riordan TJ, Dethier MN (2001) A marine plant (Spartina anglica) invades widely varying habitats: potential mechanisms of invasion and control. Biol Invasions 3(2):211–217. https://doi.org/10.1023/A:1014555516373

Haeupler H (1982) Evenness als Ausdruck der Vielfalt in der Vegetation: Untersuchungen zum Diversitäts-Begriff, 65th edn. Dissertationes botanicae, Cramer, Vaduz

Hartmann K, Stock M (2019) Long-term development in habitat characteristics and vegetation succession in an ungrazed natural versus man-made estuarine salt marsh. Estuar Coastal Shelf Sci. https://doi.org/10.1016/j.ecss.2019.106348

Hedge P, Kriwoken LK (2000) Evidence for effects of Spartina anglica invasion on benthic macrofauna in Little Swanport estuary. Tasmania. Aust Ecol 25(2):150–159. https://doi.org/10.1046/j.1442-9993.2000.01016.x

Hubbard JCE (1969) Light in relation to tidal immersion and the growth of Spartina Townsendii (s.l.). J Ecol 57(3):795–804. https://doi.org/10.2307/2258500

Huisman J, Olff H, Fresco LFM (1993) A hierarchical set of models for species response analysis. J Veg Sci 4(1):37–46. https://doi.org/10.2307/3235732

Jansen F, Oksanen J (2013) How to model species responses along ecological gradients-Huisman-Olff-Fresco models revisited. J Veg Sci 24(6):1108–1117. https://doi.org/10.1111/jvs.12050

Jensen A (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen. Denmark. Vegetatio 60(1):37–48. https://www.jstor.org/stable/20146196

Kiehl K, Jensen K, Stock M (2003) Langfristige Vegetationsveränderungen in Wattenmeer-Salzwiesen in Abhängigkeit von Höhenlage und Sedimentation. Kieler Notizen für Pflanzenkunde 30:50–68

Kiehl K, Schröder H, Stock M (2007) Long-term vegetation dynamics after land-use change in Wadden Sea salt marshes. Restor Coastal Ecosyst Coastline Rep 7:17–24

Kirwan ML, Megonigal JP (2013) Tidal wetland stability in the face of human impacts and sea-level rise. Nature 504(7478):53–60. https://doi.org/10.1038/nature12856

Knops JMH, Tilman D, Haddad N, Naeem S, Mitchell CE, Haarstad J, Ritchie M, Howe KM, Reich P, Siemann E, Groth J (2002) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293. https://doi.org/10.1046/j.1461-0248.1999.00083.x

König D (1948) Spartina Townsendii an der Westküste von Schleswig-Holstein. Planta 36(1):34–70. https://doi.org/10.1007/BF01917217

Ladd CJT, Duggan-Edwards MF, Bouma TJ, Pagès JF, Skov MW (2019) Sediment Supply Explains Long-Term and Large-Scale Patterns in Salt Marsh Lateral Expansion and Erosion. Geophysical Research Letters 46:11178–11187. https://doi.org/10.1029/2019GL083315

Lee WG, Partridge TR (1983) Rates of spread of Spartina anglica and sediment accretion in the New River Estuary, Invercargill, New Zealand. NZ J Bot 21(3):231–236. https://doi.org/10.1080/0028825X.1983.10428555

Leger EA, Goergen EM (2017) Invasive Bromus tectorum alters natural selection in arid systems. J Ecol 105(6):1509–1520. https://doi.org/10.1111/1365-2745.12852

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7(10):975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends Ecol Evol 13(5):195–198. https://doi.org/10.1016/S0169-5347(97)01286-X

Marchant CJ (1967) Evolution in Spartina (Gramineae): I. the history and morphology of the genus in Britain. J Linnean Soc Lond Bot 60(381):1–24. https://doi.org/10.1111/j.1095-8339.1967.tb00076.x

Nehring S, Hesse KJ (2008) Invasive alien plants in marine protected areas: the Spartina anglica affair in the European Wadden Sea. Biol Invasions 10(6):937–950. https://doi.org/10.1007/s10530-008-9244-z

Nolte S, Koppenaal EC, Esselink P, Dijkema KS, Schuerch M, De Groot AV, Bakker JP, Temmerman S (2013) Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies. J Coastal Conserv 17(3):301–325. https://doi.org/10.1007/s11852-013-0238-3

Nolte S, Esselink P, Bakker JP, Smit C (2015) Effects of livestock species and stocking density on accretion rates in grazed salt marshes. Estuar Coast Shelf Sci 152:109–115. https://doi.org/10.1016/j.ecss.2014.11.012

Oost AP, Hofstede J, Weisse R, Baart F, Janssen G, Zijlstra R (2017) Climate change. In: Kloepper et al S (ed) Wadden Sea Quality Status Report 2017, Common Wadden Sea Secretariat, Wilhelmshaven, p 32

Osborne B, Gioria M (2018) Plant invasions. J Plant Ecol 11(1):1–3. https://doi.org/10.1093/jpe/rtx070

Partridge TR (1987) Spartina in New Zealand. NZ J Bot 25(4):567–575. https://doi.org/10.1080/0028825X.1987.10410087

Petersen J, Kers B, Stock M (2014) TMAP Typology of Coastal Vegetation in the Wadden Sea Area. Wadden Sea Ecosyst 32, http://www.waddensea-secretariat.org

Peterson PM, Romaschenko K, Arrieta YH, Saarela JM (2014) A molecular phylogeny and new subgeneric classification of Sporobolus (Poaceae: Chloridoideae: Sporobolinae). TAXON 63(6):1212–1243 10.12705/636.19

Petruzzella A, van Leeuwen CHA, van Donk E, Bakker ES (2020) Direct and indirect effects of native plants and herbivores on biotic resistance to alien aquatic plant invasions. J Ecol. https://doi.org/10.1111/1365-2745.13380

Pielou EC (1966) The measurement of diversity in different types of biological collections. J Theor Biol 13:131–144. https://doi.org/10.1016/0022-5193(66)90013-0

Piepho HP (2004) An algorithm for a letter-based representation of all-pairwise comparisons. J Comput Graph Stat 13(2):456–466, http://www.jstor.org/stable/1391186

Proença B, Nez T, Poli A, Ciutat A, Devaux L, Sottolichio A, de Montaudouin X, Michalet R (2019) Intraspecific facilitation explains the spread of the invasive engineer Spartina anglica in Atlantic salt marshes. J Veg Sci 30(2):212–223. https://doi.org/10.1111/jvs.12720

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences 107(27):12157 LP – 12162, https://doi.org/10.1073/pnas.1002314107, http://www.pnas.org/content/107/27/12157.abstract

R Development Core Team R (2011) R: A Language and Environment for Statistical Computing. https://www.R-project.org

Ranwell D (1961) Spartina salt marshes in southern England: I. the effects of sheep grazing at the upper limits of Spartina Marsh in bridgwater bay. J Ecol 49:325. https://doi.org/10.2307/2257265

Ranwell DS (1967) World resources of Spartina townsendii (sensu lato) and economic use of Spartina Marshland. J Appl Ecol 4(1):239–256. https://doi.org/10.2307/2401421

Raybould A (2005) History and ecology of Spartina anglica in Poole Harbour. In: Humphreys J, May V (eds) The

Ecology of Poole Harbour. Proceedings in Marine Science 7:71–90, Elsevier, Amsterdam. https://doi.org/10.1016/S1568-2692(05)80011-7
Richardson D, Pyšek P, Rejmanek M, Barbour M, Panetta F, West C (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 3:14–93. https://doi.org/10.1046/j.1472-4642.2000.00083.x
Richardson DM, Pyšek P, Carlton JT (2010) A compendium of essential concepts and terminology in invasion ecology. Fifty Years Invasion Ecol Leg Charles Elton. https://doi.org/10.1002/9781444329988.ch30
Rouger R, Jump AS (2015) Fine-scale spatial genetic structure across a strong environmental gradient in the saltmarsh plant Puccinellia maritima. Evol Ecol 29(4):609–623. https://doi.org/10.1007/s10682-015-9767-6
Scholten M, Rozema J (1990) The competitive ability of Spartina anglica on Dutch salt marshes. SPARTINA ANGLICA Res Rev 7:39–47
Scholten M, Blaauw PA, Stroetenga M, Rozema J (1987) The impact of competitive interactions on the growth and distribution of plant species in salt marshes. In: Huiskes AHL, Blom CWPM, Rozema J (eds) Vegetation between land and sea: Structure and processes, pp 270–283, Springer Netherlands, Dordrecht, https://doi.org/10.1007/978-94-009-4065-9_21,
Schuerch M, Vafeidis A, Slawig T, Temmerman S (2013) Modeling the influence of changing storm patterns on the ability of a salt marsh to keep pace with sea level rise. J Geophys Res Earth Surf 118(1):84–96. https://doi.org/10.1029/2012JF002471
Schuerch M, Dolch T, Reise K, Vafeidis AT (2014) Unravelling interactions between salt marsh evolution and sedimentary processes in the Wadden Sea (southeastern North Sea). Prog Phys Geogr 38(6):691–715. https://doi.org/10.1177/0309133314548746
Sheehan MR, Ellison JC (2014) Intertidal morphology change following Spartina anglica introduction, Tamar Estuary, Tasmania. Estuar Coast Shelf Sci 149:24–37. https://doi.org/10.1016/j.ecss.2014.07.006
Simberloff D (2011) How common are invasion-induced ecosystem impacts? Biol Invasions 13(5):1255–1268. https://doi.org/10.1007/s10530-011-9956-3
Stock M (2011) Patterns in surface elevation change across a temperate salt marsh platform in relation to sea-level rise. In: Karius, Hadler, Deicke, von Eynatten, Brückner, Vött (eds) Dynamische Küsten – Prozesse, Zusammenhänge und Auswirkungen, Coastline Reports, vol 17, pp 33–48
Stock M, Kiehl K, Reinke HD (1998) Salt-marsh protection in the Schleswig-Holstein Wadden Sea area. Texte-84/97, Umweltbundesamt 84:134, http://www.umweltbundesamt.de/publikationen/salt-marsh-protection-in-schleswig-holstein-wadden
Stock M, Gettner S, Hagge M, Heinzel K, Kohlus J, Stumpe H (2005) Salzwiesen an der Westküste von Schleswig-Holstein 1988–2001. Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer 15:1–239
Stricker KB, Hagan D, Flory SL (2015) Improving methods to evaluate the impacts of plant invasions: lessons from 40 years of research. AoB PLANTS. https://doi.org/10.1093/aobpla/plv028
Strong D, Ayres D (2009) Spartina Introductions and Consequences in Salt Marshes arrive, survive, thrive, and sometimes hybridize. In: Silliman B, Grosholz E, Bertness M (eds) Human Impacts on Salt Marshes: A Global Perspective, University of California Press, chap 1, pp 3–22
Strong DR, Ayres DR (2013) Ecological and evolutionary misadventures of Spartina. Ann Rev 44:389–410. https://doi.org/10.1146/annurev-ecolsys-110512-135803
Suchrow S, Jensen K (2010) Plant species responses to an elevational gradient in German North Sea salt marshes. Wetlands 30(4):735–746. https://doi.org/10.1007/s13157-010-0073-3
Suchrow S, Stock M, Jensen K (2015) Patterns of plant species richness along environmental gradients in German north sea salt marshes. Estuar Coasts 38(1):296–309. https://doi.org/10.1007/s12237-014-9810-9
Thompson JD (1991) The biology of an invasive plant: what makes Spartina anglica so successful? Bioscience 41(6):393–401. https://doi.org/10.2307/1311746
van Bernem KH, Grotjahn M, Knüpling J, Krasemann H, Müller A, Neugebohrn L, Patzig S, Ramm G, Riethmüller R, Sach G, Suchrow S (1994) Thematische Kartierung und Sensitivitätsraster im deutschen Wattenmeer Juni 1987-Juni 1993. Tech. rep., GKSS-Forschungszentrum Geesthacht, Geesthacht, https://www.hzg.de/imperia/md/content/hzg/zentrale_einrichtungen/bibliothek/berichte/gkss_berichte_vor_2003/gkss_94_10.pdf
Wanner A, Suchrow S, Kiehl K, Meyer W, Pohlmann N, Stock M, Jensen K (2014) Scale matters: impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. Agric Ecosyst Environ 182:69–79. https://doi.org/10.1016/j.agee.2013.08.014
Widdows J, Pope ND, Brinsley MD (2008) Effect of Spartina anglica stems on near-bed hydrodynamics, sediment erodability and morphological changes on an intertidal mudflat. Marine Ecol Prog Ser 362:45–57, http://www.jstor.org/stable/24872563
Wisskirchen R, Haeupler H, Adolphi K, Albers F (1998) Standardliste Der Farn- und Blütenpflanzen Deutschlands (Standard List of Ferns and Flowering Plants of Germany)