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

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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*

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 F₁-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-stands 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 (MHTspring) 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 MHTspring 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. Schuerech 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 m² 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 m²) 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 ≥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...
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 (Akaike’s 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 MHTspring 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 x 2) factorial test design as follows: frequency ~ 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 x 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 ~ 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 x 2) factorial design as follows: response ~ 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
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 MHTspring elevation. In 1989, the central niche ranged from $t \geq 63.0$ to $t \geq 6.9$ cm MHT. Until 2019, the central niche shifted and expanded towards $t \geq -48.1$ 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-

**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-preservation in binning classes of 10 cm along the elevational gradient, indicating the model’s goodness of fit. The perpendicular dotted line indicates the assumed MHTspring 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)

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 MT$_{spring}$ elevation mark. Indeed, between 1989 and 2019, the *Spartina*-zone shifted and expanded up to the MT$_{spring}$ 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 MT$_{spring}$ 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; Scholten et al. 1987; Scholten and Rozema 1990; Gray et al. 1991).
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 MHTspring 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 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 (Runwell 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 successively 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\textsubscript{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.

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**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.

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**Compliance with ethical standards**

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

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