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Elevational ranges of pioneer marsh species are site specific and likely shaped by different abiotic and biotic factors

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Abstract

Salt marshes are dynamic systems whose landscape structure and resilience to disturbance depend on bio-geomorphological interactions. The ecological niches of salt marsh plants are asserted to be organized along an elevational gradient, determining the impact of abiotic factors such as soil aeration, flooding, and salinity, which generate the typical salt marsh zonation. In the foremost (pioneer) zone, vegetation must cope with nonoptimal environmental conditions due to strong impacts of hydrodynamic forces and sedimentation and is threatened by climate change–induced sea level rise or increased storminess. To test the hypothesis that species have different elevational ranges, which are shaped by local abiotic conditions and biotic interactions, salt marsh species occurrences and covers were recorded along 65 seaward–landward transects at two study sites on the back-barrier island Spiekeroog in the German Wadden Sea, differing in topography, site age, and history. Elevations were extracted from a digital terrain model. Zero-inflated beta regression models demonstrated that species occurrence and cover are mediated by elevation in a species-specific manner. The fast colonizer *Salicornia procumbens* occurred foremost at the lowest elevations, followed by the pioneer species *Spartina anglica* and *Salicornia europaea*. The higher marsh species *Limonium vulgare*, *Atriplex portulacoides*, and *Spergularia* spp. occurred at higher elevations, indicating varying species' vulnerability to local abiotic factors. Furthermore, the individual cover of species was negatively related to the total cover of other species, possibly indicating that species-specific elevational ranges are further modified by interspecific interactions. Especially, the cover of the ecosystem engineer *Sp. anglica* mostly had negative effects on individual species cover, although positive effects on the cover of *Sa. europaea* at the eastern site. Our results provide insights into plant species responses and interactions under highly dynamic conditions in the foremost marsh zone. Knowledge about species-specific responses to their

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abiotic and biotic environment is an important prerequisite for modeling and predicting future ecosystem shifts in salt marshes under climate change.

KEYWORDS
community assembly, competition, ecological niches, ecosystem engineering, facilitation, pioneer species, salt marshes

INTRODUCTION

Salt marshes are characterized by high disturbances caused, for example, by currents and waves. In order to persist, pioneer marsh plants need to regularly (re-)colonize disturbance-generated open patches (Adam, 2002; Almeida et al., 2016; Bertness, 1991). In the foremost pioneer zone, two alternative stable ecosystem states exist in a sensitive equilibrium (Fagherazzi et al., 2006): a low-elevation, unvegetated tidal flat and a higher elevation, vegetated marsh area (Olff et al., 1997). Seed dispersal patterns and post-dispersal conditions determine species distributions and abundances of the resulting plant community (Friess et al., 2012; Lõhmus et al., 2020; Rand, 2000; Steinigeweg et al., 2023). The typical salt marsh zonation of pioneer, low, and high marsh areas is an elevation-bound characteristic emerging from hydrodynamic (tides, currents, waves), sedimentary, and vegetation-related processes and is recurring during the ecosystem development (Adam, 1990).

Lower marsh zones are shaped by species tolerances and restricted to a community assembly of disturbance-tolerant species, while upper zones are characterized by more benign conditions with increased competitive pressure (see "ecological–physiological–amplitude–concept" formulated by Minden et al., 2012; Pennings et al., 2005; Rand, 2000; Scholten et al., 1987), leading to the distinct marsh zonation along an elevational gradient (Petersen et al., 2014). During initial plant community establishment, especially facilitation and tolerances to abiotic stresses are crucial for plant growth, while competitive pressures limit plant growth under ameliorated abiotic conditions (Bertness, 1991; Bertness & Callaway, 1994; Bertness & Shumway, 1993; Jager et al., 2018). Some salt marsh species have evolved physiological traits to cope with stressful conditions, making them eligible for primary colonization (Friess et al., 2012). These species can be grouped into fast colonizers (e.g., *Salicornia* spp.) characterized by a high probability of establishment and low lateral expansion rate versus slow colonizers (e.g., *Spartina* spp.) with a lower probability of establishment and a higher lateral expansion rate (cf. Schwarz et al., 2018). As elevation mainly controls tidal inundation, hydrodynamic forcing, and sedimentation, pioneer species initially establish when accretion exceeds a critical threshold (Evans et al., 2019; Wang & Temmerman, 2013). Afterward, a positive feedback between sedimentation and vegetation growth (Marani et al., 2007; van de Koppel et al., 2005) facilitates marsh succession, that is, the development of vegetated pioneer zones with following slow transition between the pioneer zone and the lower marsh zone over time (Engels et al., 2011).

Competition becomes more relevant, when fast colonizers as annual species are replaced by slow, often perennial, colonizers (Bertness & Shumway, 1993; Lõhmus et al., 2020). Thus, competitive pressure can emerge even in the lower marsh zones that are usually colonized by disturbance-tolerant species, for example, when ecosystem-modifying species ("ecosystem engineers" sensu Jones et al., 1994) spread. This was demonstrated for the invasive *Spartina anglica*, originally introduced into the Wadden Sea in the 1920s for its positive effects on wave attenuation and sedimentation enhancement (Nehring & Hesse, 2008). This species has now colonized the pioneer zones of salt marshes throughout the entire Wadden Sea (Nehring & Hesse, 2008). *Spartina* species generate a positive feedback between increased sedimentation and wave attenuation. They are able to alter the marsh morphology and stabilize coastlines (Strong & Ayres, 2009). Intraspecific facilitation often allows *Sp. anglica* to compete against and further exclude other pioneer species (Pennings et al., 2005; Proença et al., 2019).

Many studies have observed zone-overarching community patterns and compositions along the elevational gradient and revealed that species positioning is mostly determined by physical thresholds at their seaward limit and by competition under benign conditions at higher elevations (Friess et al., 2012; Minden et al., 2012; Pennings et al., 2005; Rand, 2000; Scholten et al., 1987). Rising sea levels and increased storminess as a consequence of climate change may potentially lead to intensified disturbances such as increased removal of plant biomass by erosion or burying by sedimentation, higher exposure of tidal marsh plants to currents and waves, or habitat loss (Colombano et al., 2021; Hu et al., 2021; Lõhmus et al., 2020; Spencer et al., 2016), especially at the seaward marsh edge. Whether and how species can cope with rising sea levels depend on their relative

position in the tidal frame and the breadth of their realized niches concerning tidal inundation (Janousek et al., 2019; Russell et al., 1985). Hutchinson (1957, 1978) introduced the concept of ecological niches of species. The ecological niche is composed of two types of niches—the "fundamental niche" and the "realized niche." The fundamental niche describes a multidimensional range of environmental conditions in which a species can potentially reproduce and survive in monoculture. The "realized niche," however, is the real positioning of a species in its local environment when it is affected by co-occurrence of other species either competing for the same resources or facilitating survival under adverse conditions. The seaward boundary is determined by fundamental niche requirements, while the landside boundary is determined by species interactions (see Scholten et al., 1987). However, the seaward boundary can be shifted by facilitation if other plants reduce the stress. Understanding those species-specific realized ecological niches is essential to close knowledge gaps about the distribution of marsh species and to appropriately manage coastal wetlands.

In this study, we evaluated the spatial vegetation patterns with focus on species-specific elevational ranges in two pioneer marsh zones on the barrier island Spiekeroog, Germany, differing in terrain height as well as site age and history. We recorded species occurrence and cover to specifically investigate the effects of microhabitat variation in elevation and the importance of biotic interactions among plants within the pioneer salt marsh zone.

We hypothesized, first, that species have different elevational ranges due to varying vulnerability to abiotic conditions such as flooding duration and frequency, which are strongly associated with site elevation. We assumed that early, fast colonizers, such as *Salicornia* species, occur at lowest elevations, whereas slow colonizers such as *Sp. anglica* and higher marsh species such as *Limonium vulgare*, *Atriplex portulacoides*, or *Spergularia* spp. take over at slightly higher elevations.

Second, we expected that species-specific elevational ranges are further modified by the presence and cover of other species. While in the foremost pioneer zone, the cover of other species may positively affect the cover of individual species by providing shelter against hydrodynamic disturbances, competitive exclusion may gain in importance with increasing elevation under more ameliorated abiotic conditions. This may especially apply to the ecosystem engineer *Sp. anglica*, not only potentially stabilizing sediments and attenuating waves but also showing a strong competitive ability.

Third, by investigating two nearby sites, differing in (micro-)topography, age, and history, we asked whether it is possible to define general elevation thresholds for the studied pioneer marsh species.

MATERIALS AND METHODS

Study site

Our study was conducted in back-barrier salt marshes on the island Spiekeroog in the German Wadden Sea (Figure 1). The study sites were located in the western and the eastern part of the island (Figure 1C). The eastern spit has first attached to the western part during 1850 and the 1950s (Eitner, 1996). Salt marshes on the eastern spit did not start to develop before 1960 and are thus younger than in the west.

Salt marshes on Spiekeroog belong to the national park "Niedersächsisches Wattenmeer" and are ungrazed and follow the typical zonation of Northern-European salt marshes, that is, pioneer community, lower salt marsh, and upper salt marsh (Lõhmus et al., 2020). The pioneer community in the foremost zone of the study sites is composed of the six salt marsh species *Sp. anglica* (C.E Hubb), *Salicornia procumbens* (SM.), *Salicornia europaea* (L.), *L. vulgare* (Mill.), *A. portulacoides* (L.), and *Spergularia* spp. (L.), with *A. portulacoides* and *Spergularia* spp. indicating fluent transitions between pioneer and higher marsh zones. Depending on the site, species dominance and abundance differ.

Recording of site-specific species composition

In October 2022, species composition at both study sites was recorded in 1 m^2 plots ($n = 1790$) with a distance of 1 m between centroids along neighboring seaward–landward transects ($n = 65$). The transects had a length of 25–35 m (Figure 1C) and started at the first growth of vegetation on the mudflat. Data were recorded at low tide, that is, 3 h after and 3 h before high tide. Transect points were mapped with a Leica GG04 dGPS. We extracted site elevations from a digital terrain model (DTM, 2022) obtained from the Forschungsstelle Küste, Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN), Germany. A photograph was taken at every transect point from 1.50 m height with a cell phone's camera, from which species cover (in percentage) and occurrence (presence–absence) was estimated for each species by visual inspection.

Statistical analysis

Differences in species composition among sites

We used nonmetric multidimensional scaling (NMDS) to explore differences in species composition between the

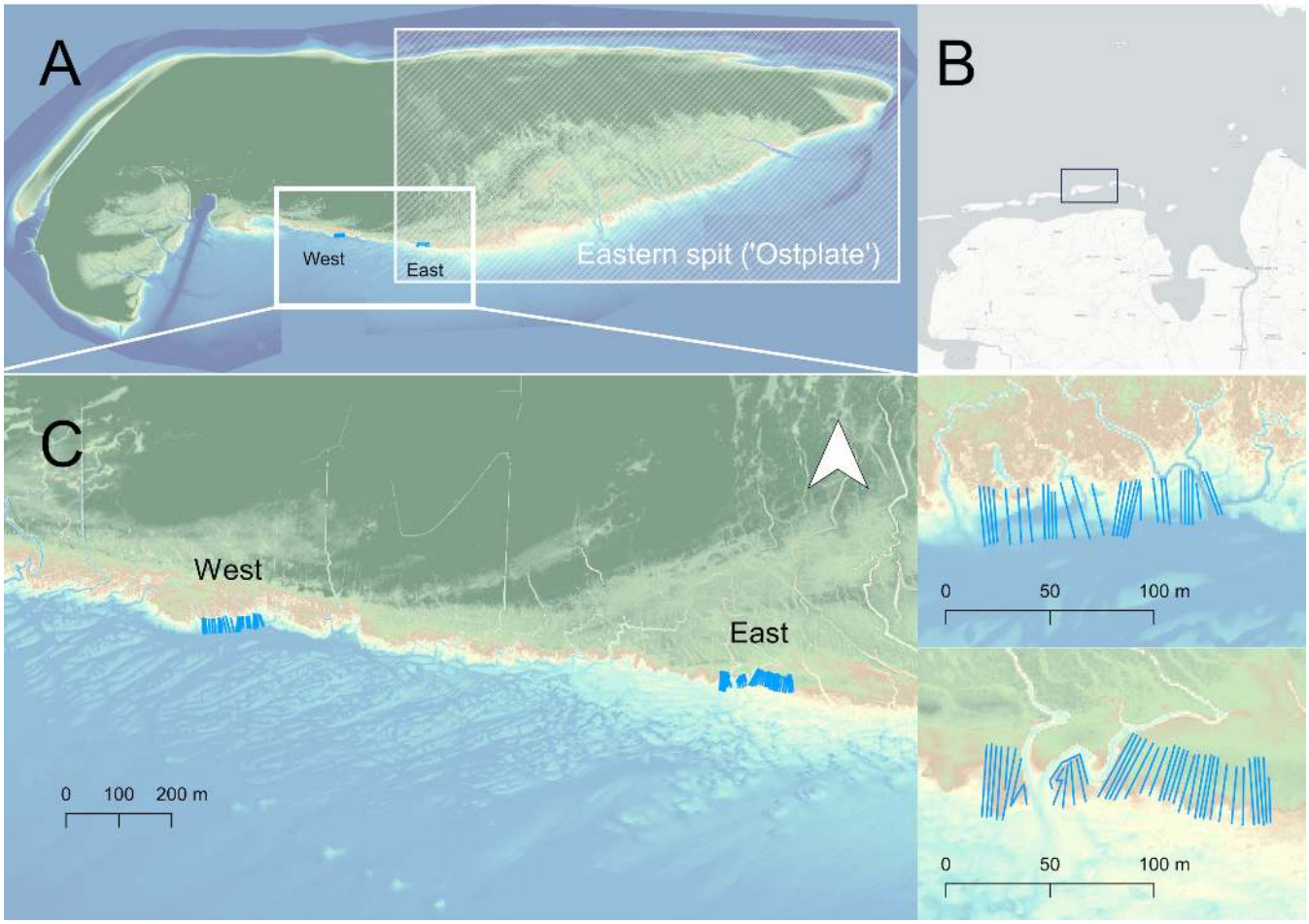


FIGURE 1 (A) The back-barrier island Spiekeroog in the North Sea, (B) German Bight which comprises an older western part and a younger eastern spit ("Ostplate," gray dashed rectangle; digital terrain model obtained from Forschungsstelle Küste [FSK], Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz [NLWKN], 2022). The study sites (C, white rectangle in A) with transects (C, blue lines) along which species cover and occurrence data were collected.

west and the east, as well as species turnover along an elevational gradient. Species cover was square root transformed because it varied widely among species. Dissimilarity indices were calculated based on the Euclidian distance, which delivered the best results in terms of stress level (0.001) as calculated based on Kruskal's stress formula (Kruskal, 1964). We used the function metaMDS() in the R-package vegan 2.6-4 (Oksanen et al., 2022) to perform the ordination. Links between species composition and elevation were explored by fitting a linear trend surface using the function envfit(). The significance of the correlation between ordination scores and elevation was tested using permutation tests ($n = 999$).

Effects of elevation on individual species cover

We used hierarchical Bayesian models with a zero-inflated beta distribution (also termed "zero-augmented beta distribution," e.g., Wright et al., 2017) to analyze the relationships between elevation and the cover of individual salt marsh species (in percentage). Statistical analyses of continuous percentages or proportions such as plant cover are not straightforward, since proportions can only take values between 0 and 1, and their variance is typically not constant (Douma & Weedon, 2019). Data transformations are often applied to be able to use standard linear modeling approaches, but may lead to biased estimates. Instead, beta regression techniques are today recommended for modeling continuous, noncount proportions such as plant cover (e.g., Damgaard & Irvine, 2019; Douma & Weedon, 2019; Wright et al., 2017). One of the main advantages of the beta distribution is the wide range of shapes it can take within the interval ($0 <$ plant cover < 1; cf. Damgaard & Irvine, 2019) allowing to model proportional data at the original scale. However, the beta distribution is not defined for exact zeros and ones. One possible solution is to add or subtract a small value from

0 and 1, respectively, especially if recorded zeros arise from detection limits. In case of a priori expectations of true zeros (or ones), that is, the absence of a plant species, zero-(one-)inflated beta regression models should be used (Douma & Weedon, 2019; Ospina & Ferrari, 2010). Moreover, the added value of zero-inflation is especially high when both zeros and relatively high proportions are observed (or both ones and low proportions in case of the one-inflation). For all study species, there were substantial amounts of plots with zero observations (43%–95%), whereas plots with 100% species coverage were not observed except for *Sp. anglica*, but even for this species, these were very few (~1.5%). Moreover, judgments of whether a plot shows a plant coverage of 99% or 100% seemed to be rather subjective and influenced by factors like wind so that the added value of one-augmentation was very low. We therefore applied zero-inflated beta regression models and rescaled proportions of *Sp. anglica* and total plant cover of 1 by subtracting a small value (cf. Douma & Weedon, 2019).

Zero-inflated beta regression models assume that the data-generating process involves two linked stochastic processes: first, the probability of observing a zero value (i.e., presence–absence of a species) is described using a Bernoulli process ("occurrence" or "zero-inflation" part of the model), and second, the percentage of plant cover itself is modeled for all nonzero observations using the beta distribution ("cover part") (cf. Douma & Weedon, 2019). The separation of the data-generating process into two independent components allows for additional inference about processes underlying occurrence, as distinct from processes determining the observed coverage of a plant (Douma & Weedon, 2019; Keim et al., 2017; Wright et al., 2017). Different predictors can be incorporated into the two model parts, and it is often useful to allow for the possibility that the precision parameter Φ (= inverse of dispersion) varies across observations as a function of covariates to account for varying variance (heteroscedasticity). Since the two study sites differed widely in species composition, probably due to different ages, history, and/or sediments, we modeled species cover for the eastern and western sites separately. Moreover, the eastern spit was on average distinctly higher than the west, with only small overlap in elevational ranges among sites.

Elevation was treated as fixed factor, potentially influencing the processes of (1) observing zeros ("zero-inflation" part) and of (2) affecting plant cover where the species occurs ("cover part"), whereas Transect ID was treated as random factor. For each species, we first fitted a null model, including intercept-only terms for the zero-inflation and cover parts, as well as for Φ. We tested both for linear and quadratic relations between elevation and occurrence as well as plant cover. We then tested extending the model by including elevation in the different parts of the model and also allowed the parameter Φ to vary with elevation. For the zero-inflation and cover parts (but not for Φ), we further tested including quadratic terms of elevation.

The models were fitted using Bayesian inference, and the inclusion of model terms was judged based on the posterior distribution of the parameters. Elevation terms were included if the 95% Bayesian credible interval (BCI) of the parameter estimate did not include zero. In addition, we calculated the Watanabe–Akaike information criterion (WAIC; Watanabe, 2010) and used leave-one-out cross-validation (LOO, based on Pareto smoothed importance sampling [PSIS], according to Vehtari et al., 2017). Both criteria aim to estimate the accuracy of the predictive distribution (Vehtari et al., 2017). Additionally, we calculated Bayesian R^2 values. In a few cases, the 95% BCI of the posterior showed a slight overlap with zero (whereas the 90% BCI did not), but models had lower LOO and WAIC than models excluding the tested covariate term. In these cases, the focal covariate term was kept in the model.

All predictor variables were standardized (subtracting the mean, dividing by SD) prior to the analysis. Logit link functions were used to relate the linear predictors to the conditional means of the zero-inflation and cover parts of the model; for the parameter Φ, a log-link was used instead. Bayesian models require setting priors for the parameters. We used brms default priors, that is, a Student-*t*-prior with three degrees of freedom and a SD of 2.5 for the intercept of the cover part of the model and for the intercept of Φ, as well as for the SD of the random effects of Transect ID. For the intercept parameter of the zero-inflation part, a logistic prior was used, being flat on the logit scale. For the regression parameters β, improper flat priors were used (ranging from $-$inf to +inf). We performed a sensitivity analysis and used normal priors with zero mean and varying variance (10 to 1000) for the regression parameters β instead, which, however, did not affect the posteriors.

Models were fitted using Stan (version 2.26.1, Stan Development Team, 2021), run through R (version 4.2.1, R Core Team, 2022) using the package brms (version 2.19.0, Bürkner, 2017). This package provides an interface that allows coding Stan models in conventional R-syntax. We always ran three chains with 10,000 iterations with a burn-in of 5000 iterations, leaving 15,000 Markov chain Monte Carlo (MCMC) samples for each parameter of each model. To check chain convergence, we visually inspected trace plots and Gelman–Rubin diagnostic plots (Gelman & Rubin, 1992). Further, we visually inspected posterior predictive distributions for systematic deviations of the predicted from the observed data.

Effects of total cover on individual species cover

In order to investigate whether the cover of the other species modifies species-specific elevational ranges, we tested whether extending the elevation models by inclusion of the cover of other species as predictor improved model fit. Further, since *Sp. anglica* is known as an environmental engineering species with potentially strong competitive ability, we specifically tested whether the cover of this species had an effect on the individual cover of the other study species. When used as predictors, the cover covariates were all square root transformed. Judgments about including a covariate term were again based on the BCI, as well as on the LOO and WAIC criteria.

RESULTS

Differences in species composition among sites

The NMDS ordination diagram showed that species composition and cover differed among the western and eastern site; separation of sample plots was mainly driven by the presence and cover of *Sp. anglica* (Figure 2). Whereas *Sp. anglica* clearly dominated in the west, the community was more diverse and scattered in the east. Ordination scores were significantly correlated with elevation ($p = 0.001$, $R^2 = 0.23$).

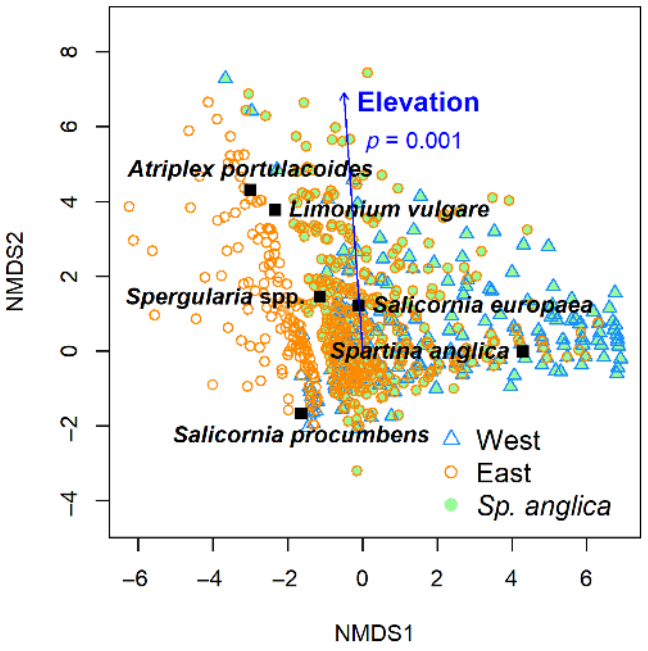


FIGURE 2 Nonmetric multidimensional scaling (NMDS) ordination plots, based on a Euclidian distance matrix of square-root-transformed cover data ($n = 1729$, $n_{\text{Transects}} = 65$), showing differences in species composition between the west and the east. The green filled marks indicate plots with *Spartina anglica* growth. The length of arrows is proportional to the correlation between the NMDS ordination scores and the elevation. The stress value (0.095) indicates an accurate representation of the dissimilarity among vegetation samples.

Effects of elevation on pioneer species cover

Despite the clear differences in elevation among the west and the eastern spit, the same elevational zonation of species was obvious (Figure 3). The lowest areas were occupied by *Sa. procumbens*, followed by *Sp. anglica* which generally showed the broadest elevational range among the pioneer species. At higher elevations, *Sa. europaea* occurred followed by *L. vulgare*, *Spergularia* spp., and *A. portulacoides*. The species with the lowest abundance in both the east and the west was *Sa. procumbens*. In the east, modeled species-specific covers were all below 10%, except for *A. portulacoides* which reached up to 22%. In the west, *Sp. anglica* cover increased up to 68%, whereas this species covered at maximum 5.5% in the east. Moreover, models including elevation as sole predictor explained 43% of the variance of *Sp. anglica* cover in the west, but only 3% in the east. The tendency of lower explanatory power of elevation in the east than in the west was also observed for *L. vulgare* and *Sa. europaea*.

The maps of predicted plant cover generated from the elevation models reflected both the different elevational ranges of the species and site-specific differences (Figure 4). The pioneer species *Sp. anglica* and *Sa. europaea* showed similar cover maps (but with *Sa. europaea* having much lower cover), whereas *Sa. procumbens* occurred in visibly lower areas, appearing to avoid sites with higher cover of the other species (Figure 4). Among the higher salt marsh species, *A. portulacoides* and *Spergularia* spp. were predicted to cover similar areas, whereas *L. vulgare* seemed to occur in a broader area.

Effects of total cover on individual species cover

The effects of the cover of other species on individual species cover differed among sites (Figure 5). In the west, we exclusively observed negative relations between the cover of a species and the cover of all other species. These effects tended to be stronger for the slow, perennial colonizers *Sp. anglica* and *L. vulgare* than for the fast

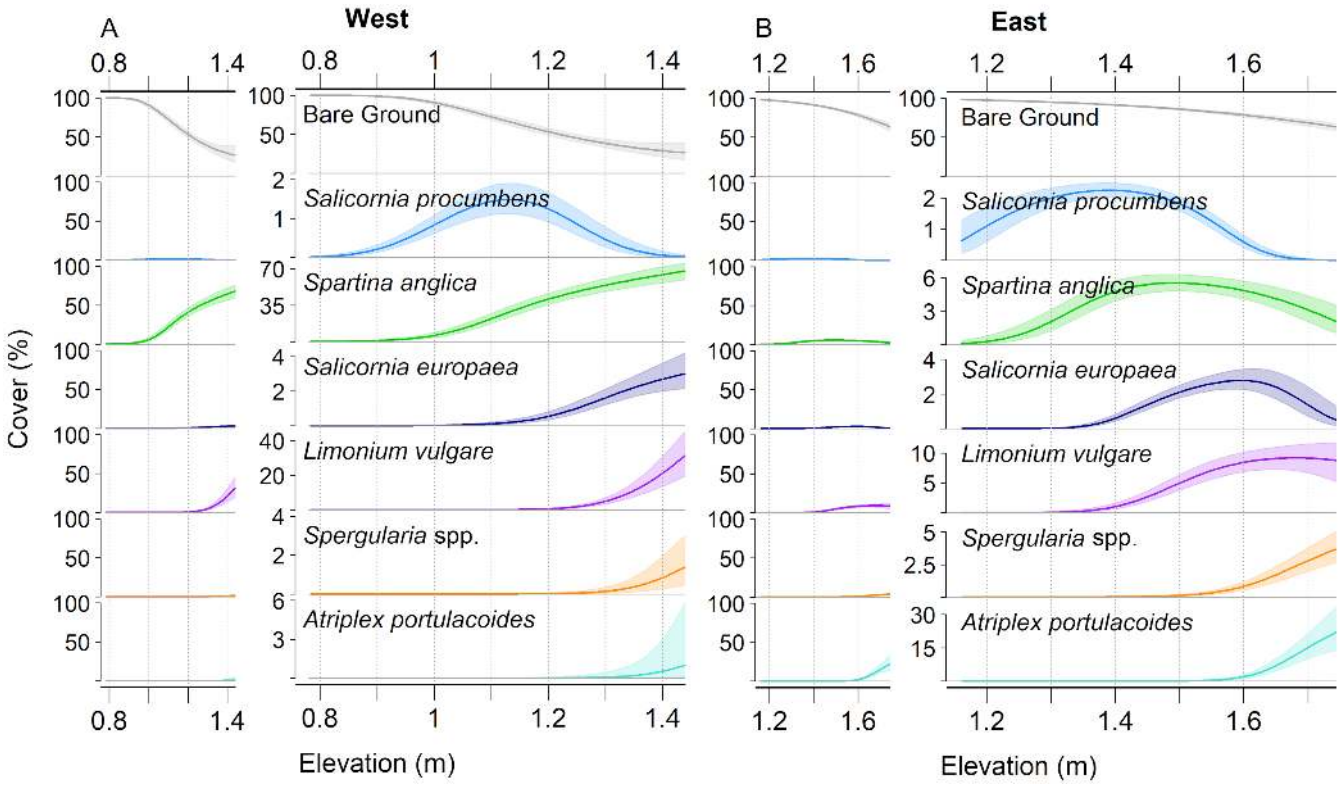


FIGURE 3 Effects of elevation on pioneer species cover. Elevation generally increased from the seaward to the landward side of the pioneer zone. Modeled species' cover in relation to elevation, estimated using hierarchical Bayesian models with a zero-inflated beta distribution (95% Bayesian credible intervals are shown). Models were fitted for each species, and (A) the west and (B) the east, separately. The *y*-axis of the left panel ranges between 0% and 100%, while the *y*-axis of the right panel varies for both models. Elevation was treated as fixed factor, and transect ID ($n = 65$) as random factor. Posteriors of parameter estimates and Bayesian R^2 values are given in Appendix S2.

colonizers *Sa. procumbens* and *Sa. europaea* (Figure 5A). We did not observe any significant effects of the cover of other species on the cover of *A. portulacoides* and *Spergularia* spp., possibly as these species were too rare at our sites.

In contrast, at the eastern site, the cover of *Sa. europaea* was positively related to the cover of other species (Figure 5B). At low to mean elevations, *Spergularia* spp. cover increased with the cover of other species, whereas the opposite was true at higher elevations. *Sa. procumbens*, *Sp. anglica*, *L. vulgare*, and *A. portulacoides* again all decreased with increasing cover of other species, but the slope of the response curves was often less steep than in the west.

Considering solely the effects of the cover of *Sp. anglica* on the cover of the other species showed a rather similar picture (Figure 6). Overall, the explanatory power of models including the cover of *Sp. anglica* was slightly lower than that of models including the cover of all other species, except for *Sa. europaea* at the eastern site (Bayesian $R^2_{\text{total cover}} = 0.15$, Bayesian $R^2_{\textit{Spartina anglica}\ \text{cover}} = 0.19$, see tables in Appendix S4). In the west, the cover of *Sa. procumbens*, *Sa. europaea*, and *L. vulgare* all decreased with an increasing cover of *Sp. anglica* (Figure 6A), although this effect was only slight in *Sa. europaea*. In the east, the cover of *Sp. anglica* was again negatively associated with the cover of *Sa. procumbens* and *L. vulgare*, but positively with the cover of *Sa. europaea* and at low to medium elevations even with the cover of *Spergularia* spp. (Figure 6B).

DISCUSSION

Our results suggest that species occurrence and cover are mediated by elevation in a species-specific manner. As hypothesized, the fast colonizer *Sa. procumbens* occurred foremost at the lowest elevations, followed by the pioneer species *Sp. anglica* and *Sa. europaea*. The higher marsh species *L. vulgare*, *A. portulacoides*, and *Spergularia* spp. occurred at higher elevations, with *L. vulgare* colonizing a wider range than the locally rare species *A. portulacoides* and *Spergularia* spp.

The individual cover of all species, except of *Sa. europaea*, was negatively related to the total cover of other species, indicating that species-specific elevational ranges are further modified by interspecific interactions.

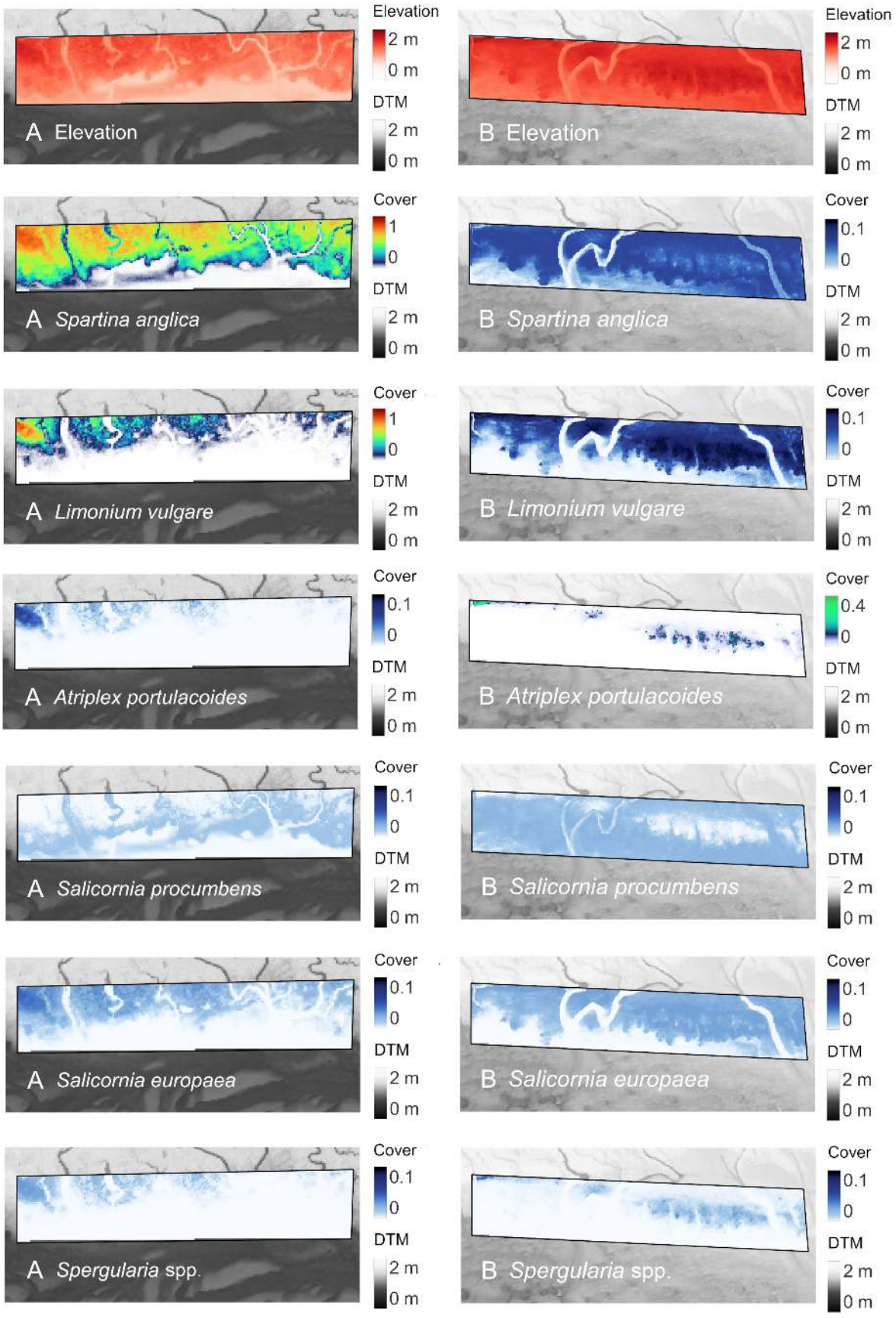


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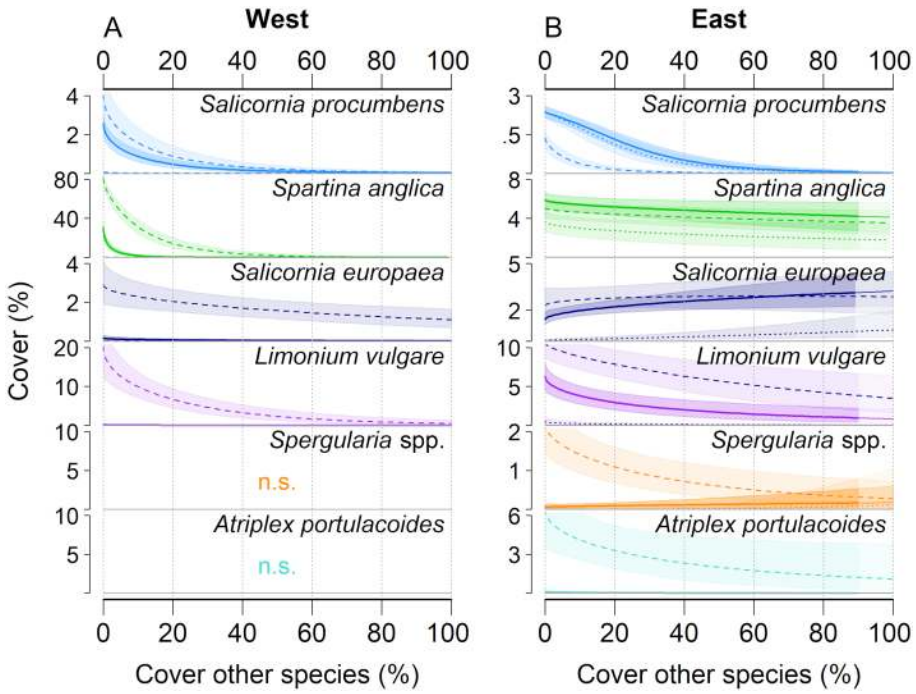


FIGURE 5 Conditional effects of the cover of other species on the cover of the studied pioneer species, estimated using hierarchical Bayesian models with a zero-augmented beta distribution (95% Bayesian credible intervals are shown). Besides the cover of other species, models included elevation as predictor (solid line, elevation set to the mean; dotted line, the 10% quantile; and dashed line, the 90% quantile). Models were fitted for each species and for the (A) western and (B) eastern pits, separately. Note that the mean elevation varied between the western (mean = 1.09 m, 10% = 0.86 m, 90% = 1.30 m) and eastern sites (mean = 1.49 m, 10% = 1.34 m, 90% = 1.62 m). Cover and elevation were treated as fixed factors, and transect ID ($n = 65$) as random factor. Predictions beyond the observed data range are plotted in brighter color. Posteriors of parameter estimates and Bayesian R^2 values are given in Appendix S3.

Especially, we observed negative effects of the ecosystem engineer species *Sp. anglica* on individual species cover, but positive effects on the cover of *Sa. europaea* at the eastern site. This supports findings from previous studies (e.g., Proença et al., 2019) that both competitive exclusion and facilitation are important processes in pioneer marsh zone development.

Species' elevational ranges

As hypothesized, species showed individual elevational ranges (Figure 3) that varied between the study locations. However, the order in which the species occurred along the elevational gradient was the same at both sites (Figure 3). The fast colonizer *Sa. procumbens* occurred at the lowest elevations, followed by the pioneer species *Sp. anglica* and *S. europaea*. The other species *L. vulgare*, *A. portulacoides*, and *Spergularia* spp. that are typically assigned to higher marsh zones occurred at higher elevations. This is in agreement with Silvestri et al. (2005), who found strong dependencies of different species' frequencies on elevation at elevation levels of 0–50 cm above mean sea level in the Venice Lagoon, Italy. Similarly, Rasser et al. (2013) observed strong associations between species distribution and elevation in Nueces marshes, Texas. The authors attributed these patterns to abiotic factors known to be coupled with bed elevation such as inundation frequency (e.g., Bornman et al., 2008). Our elevational gradient covered only a part of the whole elevational gradient in salt marshes, generating the typical zonation. Along our elevational gradient (seaward to landward), species' organization is associated with decreasing stress induced by abiotic disturbances from the lower to the higher marsh zones (Pennings et al., 2005). Species that are growing more landward at higher elevations are known to be more vulnerable to abiotic stresses typical for the foremost pioneer zone

FIGURE 4 Predicted coverage of the studied pioneer species based on the zero-inflated beta regression Bayesian models solely including elevation as predictor. Properties of the models are summarized in Figure 3 and Appendix S2. The sampling area was expanded along the marsh–tidal flat transition for both the (A) western site and (B) eastern site. DTM, digital terrain model.

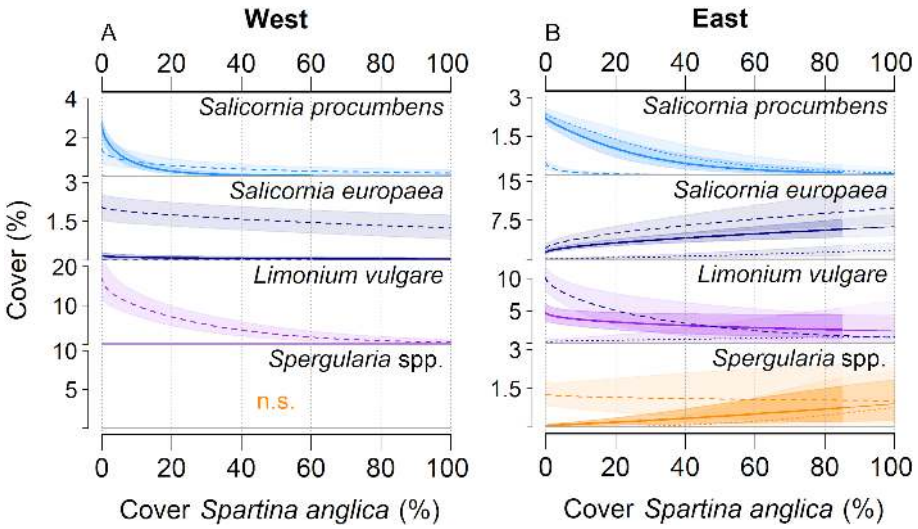


FIGURE 6 Conditional effects of the cover of *Spartina anglica* on the cover of other pioneer species, estimated using hierarchical Bayesian models with a zero-augmented beta distribution (95% Bayesian credible intervals are shown). Besides the cover of *Sp. anglica*, models included elevation as predictor (solid line, mean elevation; dotted line, 10% quantile; dashed line, 90% quantile). Models were fitted for each species, and for the (A) western and (B) eastern pits, separately. Cover of *Sp. anglica* and elevation were treated as fixed factors, and transect ID ($n = 65$) as random factor. Posteriors of parameter estimates and Bayesian R^2 values are given in Appendix S4. We did not observe any significant effects of *Sp. anglica* cover on cover of *A. portulacoides*, and for *Spergularia* spp. at the western site. Conventions were as in Figure 5.

(Bertness & Pennings, 2000; Pennings et al., 2005; Scholten et al., 1987). Pennings et al. (2005), for instance, showed that the upper marsh species *Juncus roemerianus* performed poorly in the *Spartina* zone due to its vulnerability to flooding and salinity, irrespective of the presence of neighbors. Thus, higher marsh species like *J. roemerianus*, or *L. vulgare*, *A. portulacoides*, and *Spergularia* spp. in our study, may have a lower elevation limit beyond which they cannot survive due to harsh abiotic conditions. Since our study was restricted to the pioneer zone, we did not observe any upper elevation limit for *L. vulgare*, *A. portulacoides*, and *Spergularia* spp. (Figures 3 and 4).

We even found varying elevational ranges among the disturbance-tolerant pioneer species *Sp. anglica*, *Sa. procumbens*, and *Sa. europaea* (Figure 3). As fast colonizers with high seed production, *Sa. procumbens* and *Sa. europaea* are characterized by a high probability of establishment (Schwarz et al., 2018). Both colonizer species can facilitate the establishment of perennial species such as *Sp. anglica* and *Puccinellia maritima*, for example, by trapping their vegetative tillers (Davy et al., 2001; van Regteren et al., 2020). Despite their similar life cycle traits, the elevational range of *Sa. europaea* was shifted upward compared to *Sa. procumbens* (Figure 3). This indicates that tolerance to disturbance and flooding nevertheless varies between these pioneer species and/or that other factors are also crucial for the occurrence of marsh species. A possible explanation is that whereas *Sa. europaea* grows more erect, *Sa. procumbens* is more flexible, leaning with the currents. Experimental studies are required to identify the causes of different elevational ranges of the *Salicornia* species studied.

The elevation gradient, however, is not only correlated with abiotic disturbances like flooding duration and frequency but also with varying soil properties (Pennings et al., 2005). Soil characteristics such as moisture, salinity, organic matter, and aeration can vary significantly with bed elevation and between seasons (Adam, 2002), creating different habitats that support diverse plant communities. For example, the organic carbon and nitrogen content can increase with bed elevation and lower inundation frequency (Spohn et al., 2013), whereas soil salinity decreases (Silvestri et al., 2005), providing an additional explanation for the typical vegetation zonation in salt marshes (Steinigeweg et al., 2023). Within the pioneer zone, increasing soil aeration with increasing elevation may be even more important than varying salinity. However, studies on the specific processes driving these soil changes and their impact on the vegetation are scarce. Whereas elevation may be used to approximate future vegetation changes in saltmarshes, further research is needed to disentangle the causal mechanisms shaping vegetation pattern in salt marsh ecosystems.

The effect of cover of other species on the individual plant cover

For *Sa. procumbens* and *L. vulgare*, the hypothesis of negative relations between individual species cover and the

cover of other plant species could be confirmed (Figure 5). As mentioned above, *Sa. procumbens* often grew seaward in front of the other species, possibly to avoid competition for space and nutrients (Figure 3). This was previously shown for *Sa. procumbens* communities in the Oosterschelde estuary, Netherlands, where *Sa. procumbens* seeds had a 60 times higher probability to produce a mature plant on unvegetated mudflats than in the salt marsh (Beeftink, 1985). Due to its ability to produce a large number of seeds, it can quickly colonize nearby bare patches without any other vegetation (van Regteren et al., 2020).

Contrarily, at the eastern site, possibly characterized by higher disturbances compared to the western site (see below), *Sa. europaea* seemed to be positively affected by the cover of other species in general (Figures 5 and 6), and by *Sp. anglica* cover in special. This may indicate that the cover of other species provides protection against disturbances, facilitating establishment, growth, and survival of *Sa. europaea* individuals. Cooper (1982) observed a high shoot to root ratio of *Sa. europaea* compared to other salt marsh halophytes. Hence, at high drag forces and associated scouring in front of the pioneer zone, *Sa. europaea* may experience faster uprooting than the other pioneer species. Wiehe (1935) detected that uprooting is the major source for *Sa. europaea* seedling mortality at lower elevations. Neighboring individuals of other plants may reduce the drag force and wave energy so that *Sa. europaea* uprooting is reduced. Furthermore, the low investment in roots may be related to superficial growth and advantages for nutrition (Pearson & Havill, 1988), and maybe a strategy to evade competitive exclusion induced by dense belowground biomass.

When solely considering the cover of *Sp. anglica* as predictor variable, similar effects were apparent (Figure 6). *Sp. anglica* cover was negatively related to the individual cover of the other species, except for *Sa. europaea*. A possible explanation is the strong competitive strength of this species (Nehring & Hesse, 2008). Proença et al. (2019) demonstrated high intraspecific facilitation among invasive *Sp. anglica* individuals, compared to the native *Sp. alterniflora*. Although both species covered the same niche, *Sp. anglica* was able to prevail due to higher investment in belowground biomass, that is, rhizomes, potentially increasing its colonization ability and the ability to fill empty niches. Presumably, *Sp. anglica* also competes subterraneous with other clonal species such as *A. portulacoides*, which also can occur in monospecific stands (Bouchard et al., 2003), or *L. vulgare*, which mainly reproduces vegetatively rather than sexually (Boorman, 1968). The high belowground and aboveground biomass of *Sp. anglica* may result in a limited root spacing area and nutrient availability, and thus competitive exclusion of other pioneer species.

High competitive strength when once established may explain the almost monospecific stands of *Sp. anglica* in the western part of Spiekeroog (Figure 6). In contrast, the eastern site is characterized by only edge-forming *Spartina* swards and an overall low cover, and nearly equivalent growth of *Salicornia* spp., *L. vulgare*, and *A. portulacoides*. The higher elevations of the eastern compared to the western site probably offer *L. vulgare* and *A. portulacoides* beneficial conditions to spatially expand without strong competition pressure from *Sp. anglica*. Furthermore, these results may indicate an effect of different history of the study sites. The dominant growth of *Sp. anglica* in the western part of Spiekeroog may be attributed to the active planting of this species for coastal protection measures in the 1920s in the Wadden Sea, at a time when the eastern spit did not yet exist, followed by a fast spread and dominant stands in the majority of pioneer zones (Esselink et al., 2017; Nehring & Hesse, 2008). The eastern spit was conversely able to develop without human activity after connecting with Spiekeroog in the 1950s, which may have led to a more diverse and open plant community.

Site-specific characteristics

The study sites at Spiekeroog did not only vary in their age and history but also in average bed height (Appendix S1: Figure S1) and (micro-)topography (Appendix S1: Figure S2), providing additional explanations for the difference in species coverages (Figures 4 and 5). The western study site lies evidently lower under the mean high tide (MHW) of Spiekeroog with more a variable micro-topography (Appendix S1: Figure S2) than the eastern spit. Wang and Temmerman (2013) suggested that plant growth is limited to areas lying >0.5 m under MHW. The western part, thus, may not everywhere fulfill the requirements for initial plant growth. Moreover, a flat depression running parallel to the shoreline in front of the *Sp. anglica* stand traps incoming seawater during high tide (Figure 1; Appendix S1: Figure S2; personal observation of authors). This reduces the time free from hydrodynamic disturbances that a plant needs for successful establishment (see "Windows of Opportunity"; Balke et al., 2011, 2014).

The eastern spit is less heterogenous with elevations generally higher than in the western part and with a fluent transition between salt marsh vegetation and the neighboring tidal flat. It is especially colonized by *Sa. procumbens* as first colonizer, usually making flooding conditions in the entire foremost marsh zone

potentially bearable for species. Nevertheless, we observed a significantly higher proportion of bare ground than the western site indicating higher ecosystem disturbances (Figure 3). Usually, vegetation can recover in a natural regeneration process, and bare patches are not necessarily persistent (Wang et al., 2022). However, unsuitable conditions hindering key stages in the plant life cycle can stop the ecosystem from regeneration, for example, by seed washing or reduced growth caused by abiotic stressors (Wang et al., 2022).

Conversely, the growth of the plants can also affect the site characteristics. For instance, the cover of *Sp. anglica* appears to modify the topographic structure of a site. The elevation at both sites increases noticeably at *Sp. anglica* swards compared to the bare tidal flat, supporting the suggested ecosystem engineering capacity of this species (Nehring & Hesse, 2008). Increased bed elevations have been explained by the sediment trapping ability of *Sp. anglica*. Moreover, it is likely that *Sp. anglica* also attenuates wave energy and stabilizes sediments, improving the habitat conditions for the other species growing behind.

Conclusion

To conclude, we observed varying elevational ranges of six different halophytes growing in the foremost zone of a back-barrier salt marsh in the German Wadden Sea. Possibly, species' elevational ranges were mainly shaped by differences in species' sensitivity to hydrodynamic disturbances and associated factors, for example, the temporal variations in salinity. However, interspecific interactions as well as other site characteristics can potentially shift the realized niche on the elevational gradient upward or downward and determine the niche width. Species-specific, realized niches may indicate crucial thresholds that are important to understand for predicting species vulnerability to changing conditions. We further observed that species' responses have to be locally assessed because they differ already among sites lying less than 1 km apart.

In general, our ability to predict ecosystem changes is still limited as the coupling of vegetation establishment, hydrodynamics, and sedimentation may be nonlinear (Fagherazzi et al., 2006; Kirwan & Megonigal, 2013; van Belzen et al., 2017). Especially in the foremost marsh zone, thresholds are indeed fundamental to identify tipping points marking state shifts (e.g., "critical slowing down"; cf. van Belzen et al., 2017). Considering species- and site-specific elevational ranges and growth thresholds may help to assess salt marsh stability under climate change.

AUTHOR CONTRIBUTIONS

Charlotte S. Steinigeweg designed the study and gathered the data with Ole J. Siebeneicher. Swantje Löbel conceived the statistics. Charlotte S. Steinigeweg and Swantje Löbel interpreted the data and wrote the manuscript. Swantje Löbel, Michael Kleyer, Kertu Lõhmus, Boris Schröder, and Ole J. Siebeneicher edited the manuscript. All authors have contributed to the article and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Steinigeweg et al., 2024) are available from the Technische Universität Braunschweig repository: https://doi.org/10.24355/dbbs.084-202404161050-0.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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