



Spatial and temporal patterns of initial plant establishment in salt marsh communities

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Abstract

Questions: How are dispersal processes, abiotic and biotic interactions determining the initial salt marsh plant community establishment and development when connectivity is different? We aim to answer this question by analysing the spatial and temporal patterns of plant establishment along an environmental gradient at two connectivity settings.

Location: Back-barrier salt marsh and tidal flats of Spiekeroog, northwest Germany.

Methods: We established an experiment along a saltmarsh elevation gradient with bare sediment open for spontaneous colonisation on the natural salt marsh and on the experimental salt marsh islands built on the tidal flats approximately 500 m from the natural salt marsh for low connectivity. Plant establishment was identified from georeferenced photos at least monthly.

Results: Experimental islands as low-connectivity plots had limited colonisation by annual halophytes that produced large number of small seeds. Number of individuals increased with higher connectivity at patches enclosed by salt marsh. Number of individuals was highest at the mid elevations whereas peak species richness was at the upper salt marsh. Temporal patterns of seedling emergence showed increasing plant numbers until the end of April followed by a gradual decline over the season at the pioneer and lower salt marsh zones. Upper elevations on the other hand had a stable number of low individual counts over time. Spatial clustering of plant individuals indicating possible facilitation was important at the initial stages of salt marsh development at pioneer and lower salt marsh elevation, but only early in the season.

Conclusions: Stochastic patterns of early salt marsh colonisation indicated that success of species colonisation was determined by seed properties, seed availability and environmental conditions mediated by elevation. We found indications that at the initial stages, further colonisation was supported by already colonised plants but shifted to avoidance later in the season.

KEY WORDS

community assembly, competition, dispersal, facilitation, species sorting, Wadden Sea, zonation

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1 | INTRODUCTION

The long-term stability and resilience of ecosystems depends partially on the species' ability to recover and regenerate after disturbances, which is realised by colonisation and establishment (Loreau *et al.*, 2003; Leibold *et al.*, 2004). Plant communities in active sedimentary environments such as salt marshes, are subjected to frequent physical disturbance and benefit from this ability to re-colonise disturbed areas (Adam, 2002; Leonardi *et al.*, 2016; Almeida *et al.*, 2017). Salt marshes are globally under pressure from anthropogenic developments and accelerated sea-level rise (Adam, 2002; Gedan *et al.*, 2009; Kirwan *et al.*, 2016). Additionally, frequent physical disturbance due to storm erosion and burial of plants by flotsam and sediment play a crucial role in structuring salt marsh communities (Reed *et al.*, 2018; Schuerch *et al.*, 2018). Establishment, resilience and long-term stability of salt marshes is, therefore, highly dependent on the species' abilities to re-colonise and establish after disturbances at different scales. Understanding the species-specific dispersal and re-colonisation pattern is therefore important to conserve salt marsh biodiversity but also for the provision of regulatory ecosystem services such as coastal protection (Temmerman *et al.*, 2013; Möller *et al.*, 2014; Zhu *et al.*, 2019).

Salt marsh communities are predominantly connected through hydrochorous diaspore dispersal with tidal currents (Wolters *et al.*, 2004; Chang *et al.*, 2007). Seed traits related to hydrochory and long-distance dispersal, such as the number of seeds produced per individual and buoyancy, are thus particularly important in contributing to dispersal success (Bakker *et al.*, 2002; Chang *et al.*, 2016; Raju & Kumar, 2016). Long-distance dispersal can be mediated by shorebirds and geese, especially during migration (Tóth *et al.*, 2016; Lovas-Kiss *et al.*, 2018). Interestingly, most dispersal in salt marshes has previously been described as local with limited long-distance dispersal mainly during storm events (Chang *et al.*, 2007). Although there is evidence for successful long-distance seed transport, the seeds need to be trapped in the salt marsh and deposited at suitable microhabitats, which could be hampered during storm conditions (Chang *et al.*, 2007). Dispersal of plant species by salt water is generally understudied and specific knowledge about the dispersal distances of salt marsh species is limited (Bullock *et al.*, 2017).

Plant community assembly is not only the result of dispersal but also requires successful establishment (Rand, 2000). Colonisation therefore also depends on suitable environmental conditions for the species to germinate and establish (Morzaria-Luna & Zedler, 2007; Wolters *et al.*, 2008). For salt marsh species environmental conditions such as salinity, flooding frequency and duration determine establishment success (Veenklaas *et al.*, 2015; Edge *et al.*, 2019). The combination of environmental conditions and competitive abilities of species leads to a distinct zonation of vegetation along elevational gradients in European salt marshes (Petersen *et al.*, 2014). The pioneer zone in the lowest elevations is dominated by flood- and salt-tolerant species with little competitive ability. Upper salt marsh at the highest elevation on the other hand is dominated by less stress-tolerant species with strong competitive abilities (Pennings

et al., 2005; Minden *et al.*, 2012). Understanding the effects of fragmentation and potential dispersal and establishment limitations on species sorting along environmental gradients would further the understanding of the functioning of metacommunities in general (Grainger & Gilbert, 2016).

The first plant individuals can provide shelter from hydrodynamic forcing, shade the substrate and alleviate salt stress for newly establishing individuals, therefore facilitating further colonisation (Engels *et al.*, 2011). Facilitation is more important at the stressful end of the gradient (Maestre *et al.*, 2009). Competition on the other hand is dominating at less stressful conditions at the upper elevations, where strong competitors can outcompete most other species (Crain *et al.*, 2004; Pennings *et al.*, 2005; Wanner *et al.*, 2014). The role of competition during the initial colonisation process is nonetheless small, as strong competitors tend to be slow colonisers (Tilman, 1994). Thus, competition is expected to become relevant at later stages of community assembly, when annual halophytes are replaced by perennial turfs (Bertness & Shumway, 1993).

Sea-level rise, shifting water currents, and increasing storminess may increase formation of bare sediment patches open for plant colonisation (Feser *et al.*, 2015). We therefore aim to understand plant establishment during initial salt marsh vegetation development. This was done by quantifying the effects of seed availability, environmental conditions and biotic interactions on salt marsh vegetation assembly. We studied these effects within a metacommunity experiment, where we created isolated salt marsh patches by building experimental islands at the tidal Wadden Sea coast and "connected" patches enclosed in the natural salt marsh (Balke *et al.*, 2017). Here we evaluate the spatial and temporal patterns of colonisation along the environmental gradient of the salt marsh. Specifically, we address the following questions: (a) is plant colonisation determined by connectivity and plant dispersal traits; (b) how does the elevational gradient affect initial colonisation; (c) how are the temporal changes in plant numbers affected by the environmental conditions (i.e. elevation as a proxy for flooding and biotic interactions); and (d) does initial colonisation indicate clustering or avoidance of individuals? With this paper we provide a unique experimental *in situ* approach to metacommunity research, specifically a detailed insight into initial community assembly.

2 | METHODS

2.1 | Study area and experimental design

We set up the experiment in August 2014 on the back-barrier tidal flat and salt marsh of Spiekeroog Island in the German Wadden Sea ($7^{\circ}43'30''$ E, $53^{\circ}45'31''$ N). Spiekeroog is a barrier island with naturally developed ungrazed back-barrier salt marshes. The tidal flats near the experimental setup are predominantly sandy with a mean tidal range of 2.7 m. Mean annual temperature is 9.7°C and mean annual precipitation is 761 mm. Salt marsh vegetation on Spiekeroog follows the typical zonation of northern-European salt marshes.

Upper salt marsh at the highest elevations is dominated by *Elymus athericus*, followed by a more species-rich lower salt marsh at mid elevations with high covers of *Atriplex portulacoides* and a *Spartina anglica*-dominated pioneer zone with high frequency of *Salicornia europaea* at the lowest elevations. *Suaeda maritima* had its highest frequency at the mid elevations.

We set up six 2×2 m experimental plots at each elevational zone, i.e. upper, lower and pioneer salt marsh within the back-barrier salt marsh (i.e., representing high-connectivity conditions). These plots were first cleared of vegetation to 30 cm depth, then filled with sediment from the tidal flat and left bare for spontaneous colonisation. Sides of the experimental plots were lined with root cloth to hamper colonisation from lateral growth. An additional six plots were marked as untreated reference. From each 2×2 m replicate plot, two subplots of 1×1 m were randomly allocated for non-destructive surveys such as vegetation sampling and seedling counts, and two subplots for destructive sampling, for example soil coring.

Experimental islands were built on the tidal flat approximately 500 m from the natural salt marsh to study the colonisation patterns under more isolated conditions (i.e. low connectivity) (Balke et al., 2017). Each of six experimental islands was built with 12 steel cages of 1×1 m. Three elevational levels, with four joint cages per level, correspond to the elevations of the salt-marsh-enclosed plots and hence receive the same amount of inundation. Cage heights of 70, 100 and 130 cm correspond to the pioneer, lower and upper salt-marsh plots respectively. Each individual cage was lined with permeable geotextile to sustain the sediment, and polyethylene bags at the lower section to maintain the ground water levels comparable to that in natural salt marshes (Figure 1). We then filled the cages with sediment from the surrounding tidal flat, leaving the top 10 cm of each cage empty to allow space for natural sedimentation processes. Island sediment was then left open for spontaneous colonisation. We used sediment from tidal flats for both low- and high-connectivity plots to ensure the same soil properties and seed bank possibly stored in the sediment. However based on our own samples (data not published) and the literature (Wolters & Bakker, 2002), there is no considerable persistent seedbank of salt marsh species in

the tidal-flat sediments. A detailed description of the experimental setup is published in Balke et al. (2017).

2.2 | Data collection

We followed plant establishment on experimental plots in the growing season of 2015, after allowing for spontaneous seed transport over the autumn and winter season of 2014/2015. We set up the experiment in August 2014, i.e. before the major autumn seed dispersal time for most salt-marsh species. Species that disperse earlier in the season, e.g. *Cochlearia* spp., may therefore have had some disadvantages. To record plant numbers on the experimental plots, we photographed the plots twice in April (9.04 and 28.04) and once in each following month until August. The photos were georeferenced in ArcGIS (ESRI) using corners of the marked plots as reference points. In each photo, we marked and identified all seedlings and plant individuals. We focused on the number of individuals on the plot without following the individuals separately. Therefore we can only analyse the changes in individual numbers and not in mortality or new emergence. In addition to individual numbers we sampled the plant cover on reference and experimental plots by frequency analysis in August 2015. We used a 0.9×0.9 m counting frame divided into 0.1×0.1 m cells (omitting the outer edges of plots) where we recorded the presence of each plant species that was rooted in the particular cell.

We calculated the distance to the seed source for each species recorded on the plots, as the shortest distance from the sampled plot within the salt marsh, or on the experimental island to the salt-marsh elevational zone where the species was most frequent in the natural salt marsh. For example, for *Limonium vulgare*, a species most frequent on lower salt marsh reference plots, when growing on an upper salt marsh plot we would calculate the plot distance to the lower salt marsh zone vegetation line. The vegetation zone borders and distances to plots were identified in ArcGIS (ESRI) based on aerial images provided by The Lower Saxony Department for Water, Coastal and Nature Conservation/The Wadden Sea National Park Administration of Lower Saxony. Distance to the nearest seed

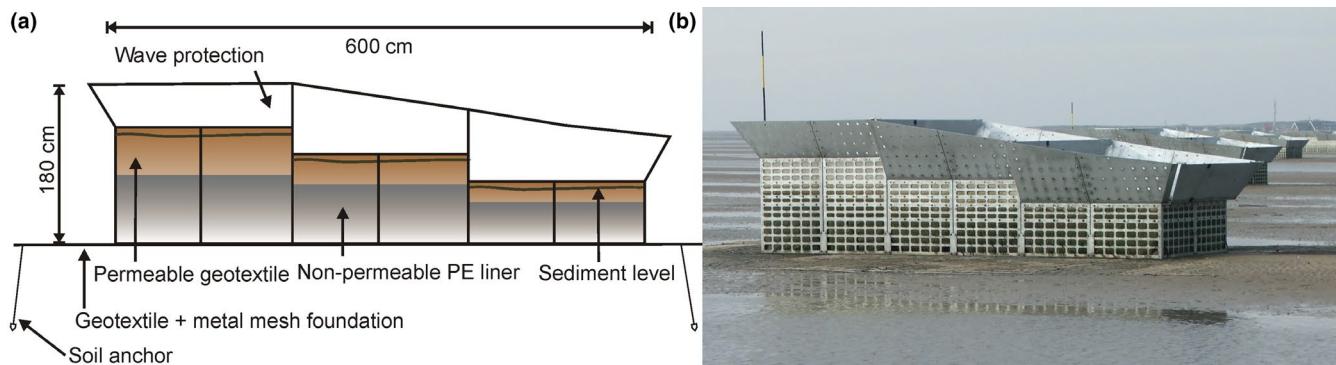


FIGURE 1 (a) Design of experimental islands with polyethylene (PE) liners to retain ground water levels and permeable geotextile to retain the sediment within the islands. Foundation of the islands is fortified with geotextile and metal gratings secured with soil anchors. Modified from Balke et al., 2017. (b) Experimental islands during low tide [Colour figure can be viewed at wileyonlinelibrary.com]

source was simplified by calculating a proxy for seed source distance based on where most of the seeds would arrive from due to the high frequency of parent plants as the direction of the dispersal vectors can change with the direction of wind and currents.

Plant trait data were collected in 2015 from 10 healthy full-grown plant individuals, when seeds were already ripe, but not yet shed. For selected plant individuals, inflorescences with seeds were clipped and stored in a paper bag. We isolated the seeds and measured the air-dried weight of all seeds and counted their number. Additional measurements for the same seed traits and species was retrieved from the LEDA database (Kleyer et al., 2008). We averaged the measured trait values per species with approximately 50 individuals per species.

Environmental conditions such as salinity and inundation frequency in the natural salt marsh and on experimental islands were monitored by Zielinski et al. (2018). We calculated the inundation duration as hours when a plot was inundated at least to the soil level (proportion of inundated hours in measured time frame) and inundation frequency as number of times the tide reached plot elevation (Appendix S1).

2.3 | Data analysis

To analyse the effect of distance from the main seed source on the number of individuals recorded on the experimental plots we fitted an exponential power model using the `lm()` function in R (R Core Team,) with log-transformed individual count as response variable and second power of distance to the seed source as explanatory variable. Only the three most frequent species were numerous enough to be analysed. We used the individual count from the point of time when the species was most frequent – end of April for *Salicornia europaea* (from here on *Salicornia*), May for *Puccinellia maritima* (*Puccinellia*) and June for *Suaeda maritima* (*Suaeda*). Trade-off between the seed mass and seed size was evaluated by reduced major axis regression (Warton et al., 2006) to aid the interpretation of plant colonisation results. Relationships between the species counts at the peak of the growing season in August and environmental parameters were investigated with non-metric multi-dimensional scaling (NMDS) using the `metaMDS` function in the `vegan` package (Oksanen et al.,). We

used Bray–Curtis distances with random starting configuration and 100 iterations, which resulted in a final two-axes solution with a stress value of 0.1.

We analysed the differences in plant numbers between the elevation zones and sampling times on salt marsh-enclosed plots using a generalised linear mixed model with Poisson distribution in the `lme4` package (Bates et al., 2015). We entered number of individuals as response variable, time and elevational zone as fixed effects and plot id as random intercept. We built separate models for *Salicornia* and *Suaeda*. Marginal and conditional R^2 following Johnson (2014) were calculated to estimate the model fit. Marginal R^2 for mixed-effect models measures the variance explained by fixed effects, conditional R^2 additionally includes the variance explained by fixed and random effects.

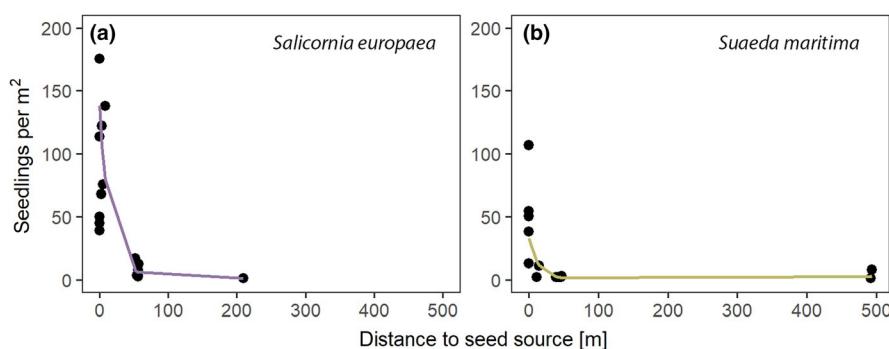
To estimate the spatial distribution of plant individuals on the salt marsh-enclosed plots we calculated Moran's I for each 1×1 m subplot using the `lctools` package in R. Moran's I measures the overall spatial autocorrelation indicating either clustering or avoidance of plant individuals. To focus on the small scales where plant interactions are taking place we divided each experimental plot into 0.25×0.25 m sections and calculated the average nearest-neighbour distance within these smaller windows using the `spatstat` package in R. We then used a generalised linear mixed model with Poisson distribution to analyse the effect of mean nearest-neighbour distance at the previous time step on the changes in plant numbers. We built models separately for each species and each zone. Mean nearest-neighbour distance between all individuals from all species and time point were used as fixed effects and plot id as a random intercept.

3 | RESULTS

3.1 | Effect of distance on species colonisation

Taking into account both high- and low-connectivity treatments, the number of plants per m^2 of *Salicornia* and *Suaeda* decreased exponentially with distance from the seed source (Figure 2). *Salicornia* (number of *Salicornia* individuals = $4.9 - 0.07 \times \text{distance} + 0.0002 \times \text{distance}^2$; $R^2 = 0.79$, $p < 0.001$) showed a similar decrease with distance as *Suaeda* (number of *Suaeda* individuals = $3.5 - 0.07 \times \text{distance} + 0.0001 \times \text{distance}^2$, $R^2 = 0.73$,

FIGURE 2 The number of individuals per m^2 depends on the distance to the seed source. Coloured lines show the number of individuals predicted from a linear model for (a) *Salicornia europaea* and (b) *Suaeda maritima* [Colour figure can be viewed at wileyonlinelibrary.com]



$p < 0.001$). Distance from the seed source did not explain the variation in individual counts of *Puccinellia*. Seed mass and seed number of salt marsh plants displayed a trade-off ($R^2 = 0.28$, $p < 0.05$). *Salicornia* is a species producing the largest number of lightest seeds, with salt marsh grasses like *Spartina anglica* and *Elymus athericus* investing in fewer larger seeds (Figure 3).

3.2 | Species establishment patterns along the elevational gradient

Abiotic factors as inundation parameters, salinity and nitrogen availability were highly correlated with elevation and their independent effects could therefore not be distinguished (Figure 4). In the following, we therefore use elevation as indication of soil salinity, nutrient availability and inundation regime. salt marsh-enclosed experimental plots were successfully colonised by 15 species, with species richness increasing with elevation (Appendix S2). The NMDS showed significant overlap of plant communities along the elevational gradient (Figure 4) with annual halophytes *Salicornia* and *Suaeda* being most abundant at all elevational levels. Species characteristic for lower salt marsh communities, e.g., *Limonium vulgare* and *Aster tripolium*, were colonising the upper elevation (Figure 4) where they did not grow in the natural salt marsh. Yet, these species remained low in frequency. As a comparison, 12 species were growing in the natural salt marsh reference plots, with most species in the lower salt marsh zone. Pioneer and upper salt-marsh zones were largely dominated by a single species, *Spartina anglica* and *Elymus athericus* respectively (Appendix S3).

In salt marsh-enclosed plots plant counts across species were largest at the middle of the elevational gradient, i.e. at the lower salt marsh elevation with a mean ($\pm SE$) of 209 ± 204 individuals per m^2 over the season and a maximum of 970 *Salicornia* seedlings per m^2 at the end of April. The mean individual number in the pioneer zone was 89 ± 138 individuals per m^2 , and a maximum of 700

Salicornia seedlings per m^2 . The upper elevation, despite having the largest species richness, had the lowest individual count with a mean of 10 ± 7 and maximum of 24 seedlings per m^2 . Average individual number for other species than the two dominating annual halophytes, i.e. *Salicornia* and *Suaeda*, remained under 11 individuals per m^2 (Appendix S2).

The experimental islands had limited colonisation with only *Puccinellia*, *Salicornia* and *Suaeda* establishing and a maximum of nine individuals per m^2 (Appendix S4). Similar to the salt marsh plots, the largest number of individuals colonised the lower elevation, followed by the pioneer elevation and with the upper elevation having the lowest number of individuals and only one species – *Salicornia*.

3.3 | Temporal changes in plant numbers

Temporal patterns were only analysed for salt marsh-enclosed plots and differed slightly between the two most frequent species (Figure 5). *Salicornia* behaved slightly different across the elevation zones ($R_m^2 = 0.86$, $R_c^2 = 0.99$), where it increased in numbers until the end of April and slowly decreased thereafter in pioneer and lower salt marsh. In the upper salt marsh no such pattern occurred; instead the number of plants remained low throughout the season. For *Suaeda*, there was no time and zone interaction, with individual numbers being smaller in April and August, but no difference at other time points ($R_m^2 = 0.89$, $R_c^2 = 0.98$).

3.4 | Spatial distribution of individuals

Plants were in general clustered in the lower salt marsh (Moran's $I = 0.23$) and pioneer zone (Moran's $I = 0.16$), but not in the upper salt marsh, where they were randomly distributed. *Salicornia* individuals were spatially clustered in the lower (Moran's $I = 0.20$) and pioneer

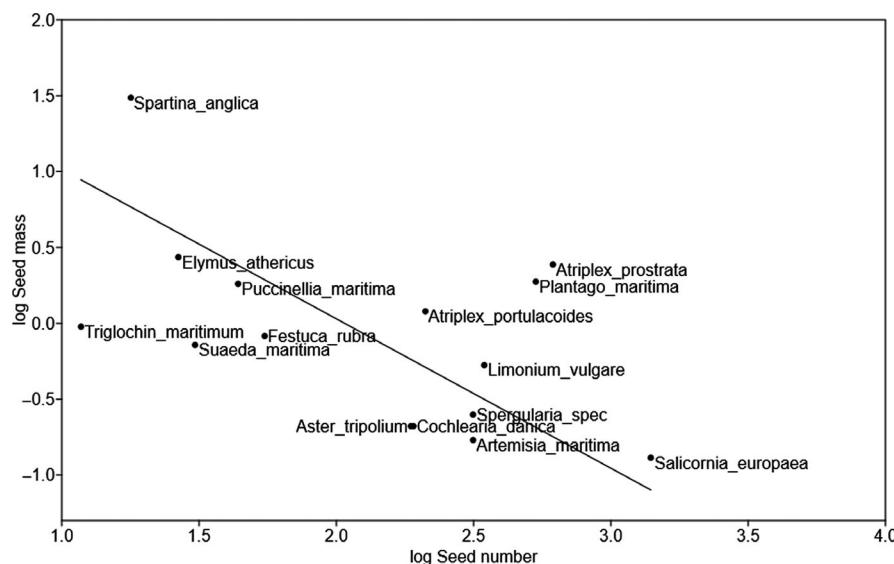


FIGURE 3 Trade-off between seed mass and seed number of salt marsh plants

FIGURE 4 Bray–Curtis-based non-metric multi-dimensional scaling (NMDS) plot of all plots (stress 0.1) shows variable vectors for environmental parameters. Triangles represent salt marsh-enclosed plots, circles experimental islands. Only three experimental islands were colonised and could be included in the analysis [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

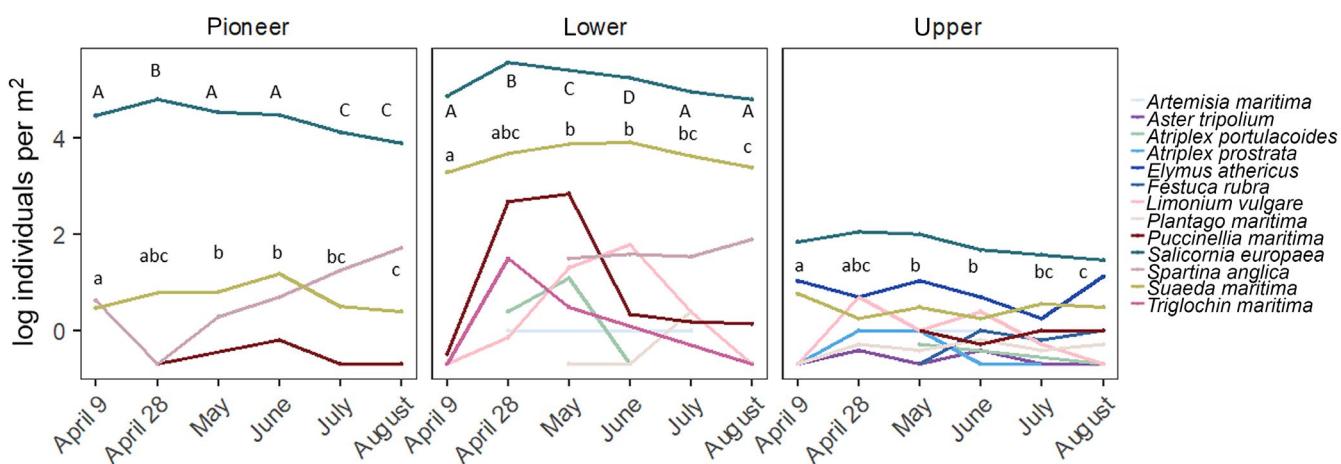
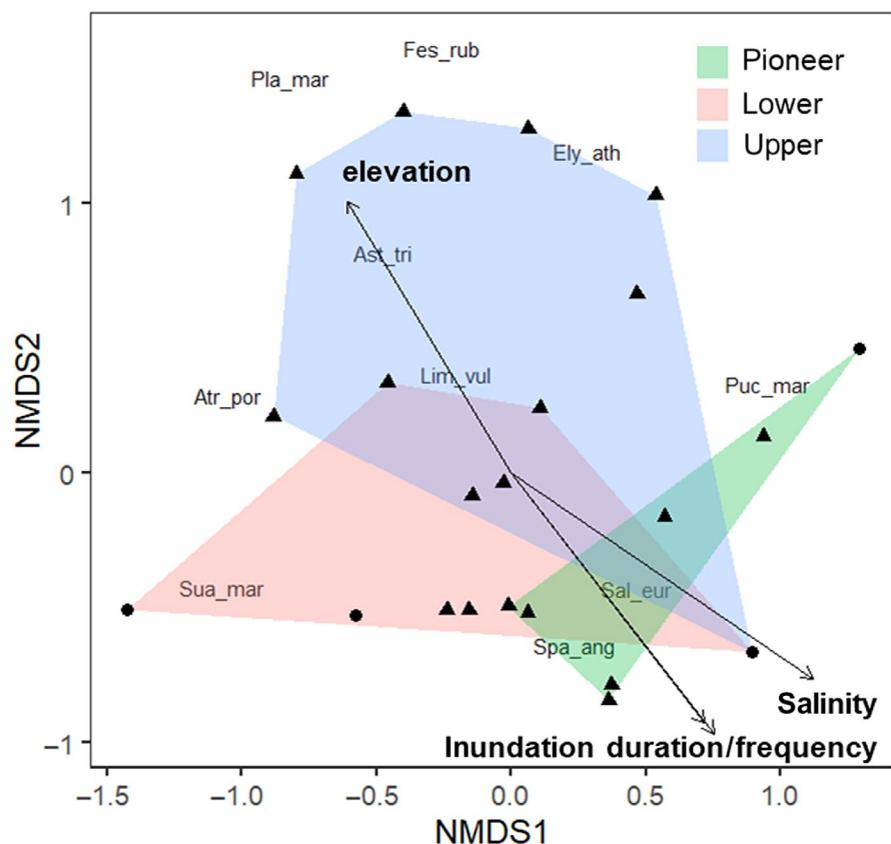


FIGURE 5 Average plant individual numbers (log) on salt marsh-enclosed experimental plots during the sampling period. Letters denote differences between time points from a post-hoc test of the generalized linear mixed model – capital letters for *Salicornia europaea* (no differences in upper zone), lowercase letters for *Suaeda maritima* [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

salt marsh (Moran's $I = 0.10$), but not in the upper salt marsh, where the individuals were randomly distributed. *Suaeda* was randomly distributed in all zones, except for the lower salt marsh (Moran's $I = 0.12$). Individual counts on the experimental islands were too low to analyse spatial patterns.

The increase in individual numbers between time steps depended on the mean nearest-neighbour distance (mnnd) for *Salicornia* in both pioneer and lower salt marsh (Figure 6). In the

first two time steps in the pioneer zone, we would see more individuals at locations where the mnnd was smaller in the previous time step. This effect, however, levels off by June. Later in the season we had more individuals at locations where there were lower mnnd values. In the lower salt marsh, we saw grouping of *Suaeda* individuals between April and May, but at other time points, there was either no effect or avoidance of already densely colonised areas (Figure 7).

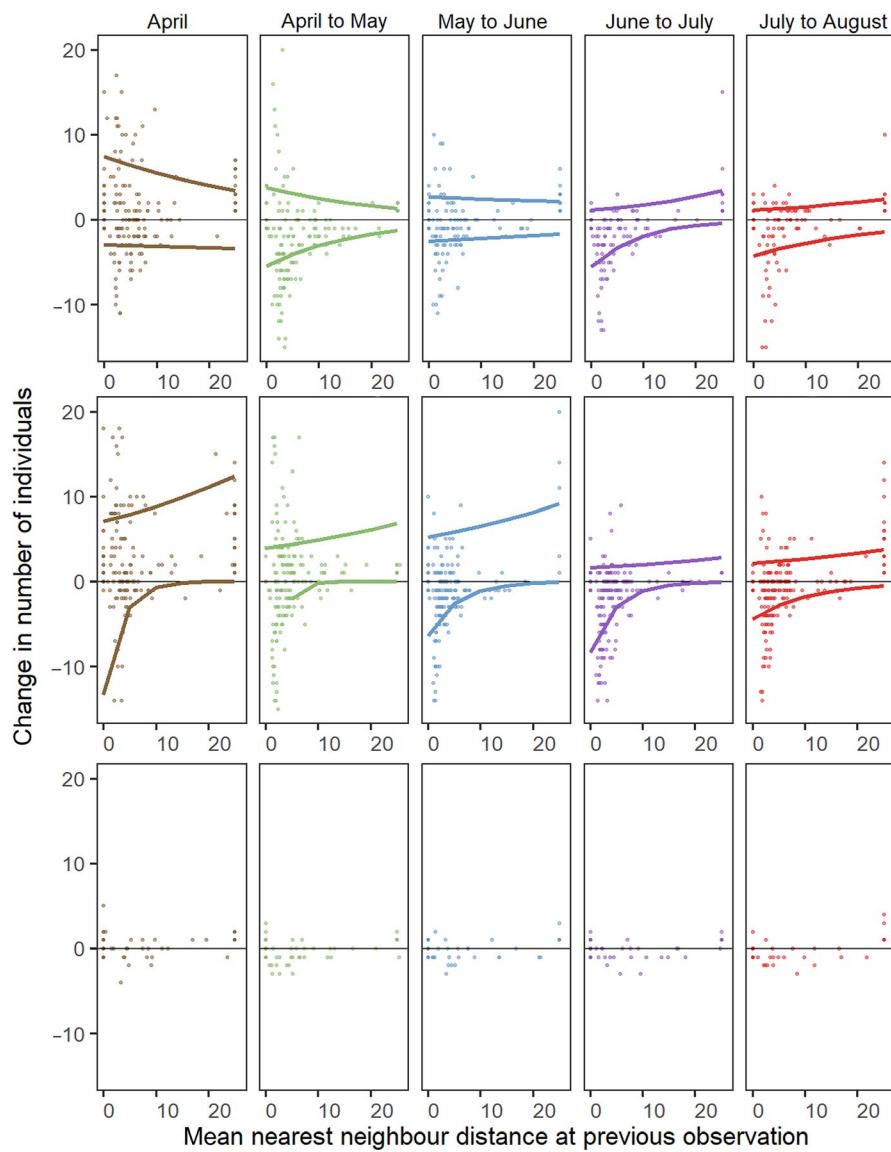


FIGURE 6 Interaction between change in number of individuals of *Salicornia europaea* and mean nearest -neighbour distance calculated for the previous time step. Coloured lines show model predictions from generalised linear mixed models [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

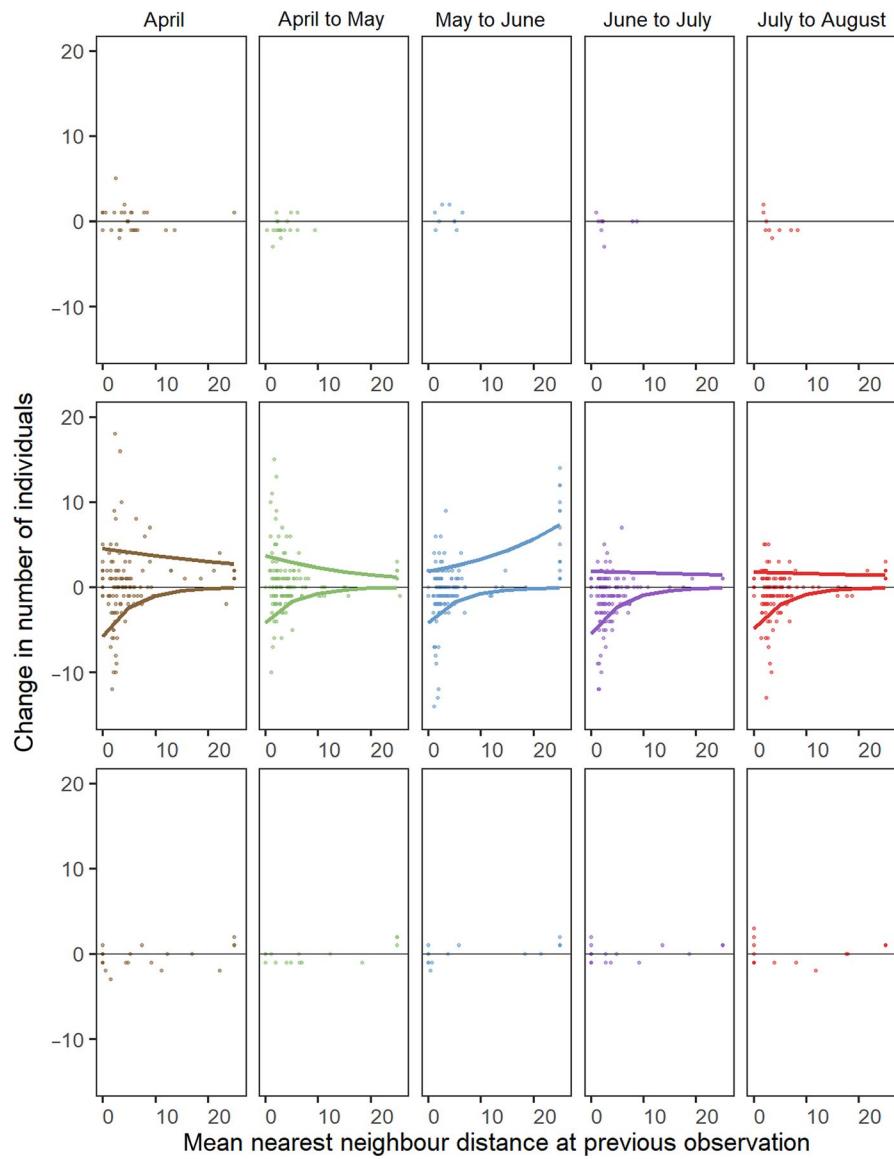
4.1 | Connectivity and role of plant traits

Connectivity of the salt marsh patches affects the initial colonisation in the recovery processes. Limited dispersal to experimental islands already at distances of approximately 500 m (Figure 2) shows that most dispersal in salt marshes takes place at relatively local scales. This has been shown previously (Chang *et al.*, 2007), but only within salt marshes, not across uninhabitable mudflats. Dispersal and establishment success results from the interplay of connectivity and traits enabling long-distance dispersal. Species with these traits were successful at reaching the low-connectivity sites. The annual halophytes *Salicornia europaea* and *Suaeda maritima* were the most numerous colonisers in our study and together with *Puccinellia maritima*, the only species that managed to colonise the more isolated experimental islands. Similar initial colonisation and domination of annual species has been noted for both restored areas and in open patches in otherwise intact natural salt marsh (Tessier *et al.*, 2002;

Hughes *et al.*, 2009; Balke *et al.*, 2017). *Salicornia* produces large numbers of very light seeds that are adapted to water dispersal (Figure 3). The seed dimorphism of *Salicornia*, where small and large seeds show varying germination responses and possibly different dispersal mechanisms, could add to the success (Ameixa *et al.*, 2016; Liu *et al.*, 2018). *Suaeda* on the other hand produces fewer slightly larger seeds that have high buoyancy (Raju & Kumar, 2016). The high germination rate of *Suaeda* seeds may further improve its success as an initial coloniser. Both *Salicornia* and *Suaeda* seedlings are also known to tolerate high salinity and waterlogging conditions (Tessier *et al.*, 2000). Although seed traits do not support *Puccinellia* as a good long-distance disperser, it has an ability to emerge from vegetative parts that can float (Bakker *et al.*, 2002). Clonal growth and establishment from displaced plant fragments is therefore another aspect in community assembly already at the initial stages.

Distance to main seed sources and reduced inundation events at the upper salt marsh elevations could lead to insufficient seed arrival within the salt marsh. Bare soil, lower soil salinity and inundation frequency suggest favourable conditions for establishment.

FIGURE 7 Interaction between changes in number of individuals of *Suaeda maritima* and mean nearest-neighbour distance calculated for the previous time step. Coloured lines show model predictions from generalised linear mixed models. [Colour figure can be viewed at wileyonlinelibrary.com]



The interplay between suitable conditions but lack of diaspores is evident from the low seedling numbers but high species diversity in the upper salt marsh zones. Even when water level reaches higher elevations, the upward transport of propagules from lower salt marsh elevations is generally lower than the seed transport from higher elevations towards the mudflats (Huiskes *et al.*, 1995; Wolters *et al.*, 2004; Zhu *et al.*, 2014). This also means that at elevations with high inundation frequency, such as the pioneer zone, a large proportion of seeds can be transported out of salt marshes into the uninhabitable mudflats at subsequent tides, again reducing the availability of seeds (Zhu *et al.*, 2014). The highest number of seedlings at lower salt marsh elevations could be the result of the location around the elevation of mean high water. The water's edge there could provide substantial input of seeds via wave-skimming, similar to the deposition of floatsam (Tessier *et al.*, 2002). The small step in elevation between high and low marsh at our study site might further encourage seeds to be stranded at that location.

4.2 | Role of environmental factors

After seed arrival, the seedling's emergence and survival are related to environmental factors such as inundation regime (Pétillon *et al.*, 2010), hydrodynamic conditions (Mateos-Naranjo *et al.*, 2008; Redelstein *et al.*, 2018), sediment stability (Bouma *et al.*, 2013; Cao *et al.*, 2018) and salinity (Shumway & Bertness, 1992; Dethier & Hacker, 2005; Hughes *et al.*, 2012). Lower water storage of the sandy tidal-flat sediments could be causing unsuitable soil moisture and salinity conditions during periods of germination, especially in the upper elevations with higher groundwater levels and infrequent inundation. Salinity on the experimental salt marsh and island plots was higher compared to the natural salt marsh conditions in the initial seed germination period (Appendix S5). *Salicornia* and *Suaeda* are better adapted to hypersaline conditions that otherwise often hamper seed germination and seedling survival for most plant species (Shumway & Bertness, 1992; Davy *et al.*, 2001; Tessier *et al.*, 2002). The hypersaline conditions at lower and upper zones at the

beginning of the growing season could therefore partially explain the dominance of those two species at all elevations. Established plants in the upper salt marsh, however, grew taller compared to the lower and pioneer zone, suggesting more suitable conditions in the upper salt marsh, instead of restrictions due to hypersalinity (Balke *et al.*, 2017). Similar better growth of halophytes at higher elevations has been observed in subarctic salt marshes (Snow & Vince, 1984). Open spaces after disturbances often enable pioneer species to grow higher in the tidal frame and should similarly support upper marsh species lower in the tidal frame (Sullivan *et al.*, 2018). However, *Elymus athericus*, a characteristic species of the upper salt marsh, did not colonise the bare patches at lower elevations. We consider this a clear indication of species sorting due to environmental stress, as shown with transplantation experiments (Bertness & Ellison, 1987; Pennings *et al.*, 2005). We did find species from lower elevations colonising bare patches in the higher marsh where they do not occur in natural salt marshes. We therefore expect that after a first strong colonisation from annual halophytes, they are replaced by more competitive species in later years (Tessier *et al.*, 2002).

The question of dispersal vs establishment on our experimental patches, however, needs additional investigation, as our current results are a combination of variation in recruitment and survival as well as dispersal. Disentangling dispersal and establishment functions is challenging due to the many factors involved and measuring dispersal is notoriously difficult and resource-consuming (Bullock *et al.*, 2006). However, the need for such dispersal studies is great, considering that knowledge about dispersal abilities of salt marsh species is limited and dispersal by water particularly understudied (Bullock *et al.*, 2017).

4.3 | Temporal patterns and biotic interactions

Salicornia achieved its largest density by the end of April and declined steadily throughout the season in pioneer and lower salt marsh zones. A similar temporal pattern of seedling emergence and decline was observed in a natural salt marsh by Jefferies *et al.* (1981). Changes in *Salicornia* at the pioneer zone showed clustering at the initial seedling establishment in April and May – increases in plant numbers were then larger at locations where mean distances between nearest neighbouring plants were the smallest. In the lower salt marsh, *Salicornia* was rather establishing at locations where there was more space available, and only between April and May were new plants emerging at locations with denser plant cover. This clustering behaviour could be an indication of facilitation at early life stages (Bertness & Leonard, 1997). Another explanation could be clustered seed deposition, but the flat and homogenous experimental plots offer little support for this assumption. Decrease of individual numbers on the other side was clearly density-dependent in the lower salt marsh, whereas in the pioneer zone this relationship was weaker and prevalent only later in the season. Intraspecific competition could occur already at the early stages of community development, if high enough densities were reached.

Similar to *Salicornia*, clustering of *Suaeda* seedlings only appeared during the main establishment phase and the decrease in numbers at the lower salt marsh seemed to be density-dependent. In the upper salt marsh plant numbers remained low but stable throughout the season. For both species, seedling increase by facilitation subsequently led to a decline by competition in lower salt marsh zones. These differences in population dynamics on small spatial and temporal scales highlight the relative importance of seed deposition vs density-dependent seedling emergence and mortality. Initial plant communities were shaped by the seed availability and biotic interactions. The importance of small-scale heterogeneity within an elevational zone will probably take effect at later stages of community development (Deák *et al.*, 2015).

Dispersal and establishment success play a crucial role in shaping salt marsh plant communities. Our results confirm that seed availability and environmental conditions determine the initial community of a salt marsh. These results further emphasise the need of restoration efforts to consider the availability of connected seed sources in the vicinity. We however need to have a better recognition of the interplay between dispersal properties and the traits of salt marsh species to cardinally widen the understanding of salt marsh metacommunities.

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DATA AVAILABILITY STATEMENT

Environmental data are available in the paper: "Environmental conditions of a salt-marsh biodiversity experiment on the island of Spiekeroog (Germany)"™, <https://doi.org/10.5194/essd-10-1843-2018>. Raw data supporting the findings of this study are stored at the University of Oldenburg and are available from the corresponding author (KL) on request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Average seedling number per m² on salt marsh and experimental island plots.

Appendix S2. Species frequency in natural salt marsh control plots.

Appendix S3. Number of plant individuals on colonised experimental islands.

Appendix S4. Flooding duration and events.

Appendix S5. Pore-water salinity during the growing season.

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