Experimental salt marsh islands: A model system for novel metacommunity experiments

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A R T I C L E   I N F O

A B S T R A C T

Shallow tidal coasts are characterised by shifting tidal flats and emerging or eroding islands above the high tide line. Salt marsh vegetation colonising new habitats distant from existing marshes are an ideal model to investigate metacommunity theory. We installed a set of 12 experimental salt marsh islands made from metal cages on a tidal flat in the German Wadden Sea to study the assembly of salt marsh communities in a metacommunity context. Experimental plots at the same elevation were established within the adjacent salt marsh on the island of Spiekeroog. For both, experimental islands and salt marsh enclosed plots, the same three elevational levels were realised while creating bare patches open for colonisation and vegetated patches with a defined transplanted community. One year into the experiment, the bare islands were colonised by plant species with high fecundity although with a lower frequency compared to the salt marsh enclosed bare plots. Initial plant community variations due to species sorting along the inundation gradient were evident in the transplanted vegetation. Competitive exclusion was not observed and is only expected to unfold in the coming years. Our study highlights that spatially and temporally explicit metacommunity dynamics should be considered in salt marsh plant community assembly and disassembly.

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1. Introduction

Species composition and ecosystem functioning in aquatic and terrestrial ecosystems cannot be understood by studying local processes alone. Local competitive and trophic interactions have to be studied in a metacommunity context as communities on habitat patches that are connected with each other by dispersal (Amarasekare and Nisbet, 2001; Holyoak et al., 2005; Leibold et al., 2004). Metacommunity theory has increasingly gained attention since the 1990s (Wilson, 1992) and amends classical ecological theory by acknowledging the spatial dynamics of species and alleviating the assumption that local communities are regulated by

local niche processes alone (Hillebrand and Blenckner, 2002; Leibold et al., 2004; Shurin and Allen, 2001). To date few field experiments have tried to investigate its basic principles despite the importance of habitat fragmentation and shifting species ranges with climate change (Logue et al., 2011; Grainger and Gilbert, 2016). Here we present the first year's results of a real scale metacommunity field experiment using salt marsh islands as a model system.

Local niche partitioning should dominate community assembly when assuming unlimited dispersal, large population size and stable environmental conditions. This means that in a heterogeneous environment species are not restricted to filling their respective niches (Leibold et al., 2004). Under dispersal limitation however community assembly may be dominated by species with high dispersal ability, especially when competitive species with poor dispersability are not able to fill in their respective niche.

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Dispersal limitation in a metacommunity may therefore lead to different or delayed assembly sequences compared to situations with unlimited dispersal (Drake, 1991; Fukami et al., 2005) and is thus suggested to affect local biodiversity (Mouquet and Loreau, 2002) and ecosystem properties (Körner et al., 2008). Environmental change often generates succession where resident (i.e. already present) species are eventually replaced by better adapted colonising species. Species composition at a given time therefore depends on the elapsed time since environmental change occurred, the persistence of the residents and the dispersal and competitive abilities of newly arriving species (Lindborg and Eriksson, 2004). Bare unoccupied patches may get colonised more rapidly by a newly arriving species compared to already occupied patches where priority effects (i.e. earlier presence of a particular species and the effect of species arrival sequences) may prevent subsequent colonisation and establishment (Loeuille and Leibold, 2008). Such usually deterministic changes in species composition may become stochastic when short term variability of the environmental conditions continuously interrupts the directional development of the community. Competitive traits and trait based sorting of species may become secondary in stochastic community assemblies.

Modelling has been the predominant tool to explore community assembly in a metacommunity context (Kneitel and Chase, 2004; Mouquet and Loreau, 2002; Shoemaker and Melbourne, 2016) with little empirical evidence (Grainger and Gilbert, 2016; Logue et al., 2011). The majority of metacommunity experiments deal with the disassembly of communities after experimental fragmentation (Haddad et al., 2015), where researchers often observe a slow decline of species richness towards a new equilibrium (Gonzalez, 2000). Only few in situ experiments have studied metacommunity assembly mechanisms exposed to stochasticity of environmental conditions (Mouquet et al., 2004; Resasco et al., 2014).

Salt marshes have increasingly gained attention in times of climate change with ongoing discussions about whether marsh accretion can keep pace with accelerated sea level rise (Kirwan et al., 2016). Within this climate change debate there is a knowledge gap about how local succession of salt marsh communities due to drowning or emergence interacts with processes at the metacommunity scale (e.g. fragmentation due to habitat loss or changes in tidal currents/dispersal vectors). The shallow tidal Wadden Sea coast is characterised by emergence and erosion of salt marsh habitat often creating small vegetated island patches disconnected from the mainland or from other back barrier islands. These salt marsh patches are only connected with each other through hydrochorous seed dispersal (Wolters et al., 2004) and species sorting is driven by an elevational gradient of flooding, disturbance and salinity (Bertness and Leonard, 1997). Salt marshes are therefore an ideal model system to study metacommunity theory as fragmentation and dispersal limitation interact with species sorting along environmental gradients.

The elevational border between tidal flat habitats with predominantly marine organisms and the habitat of terrestrial salt marsh plant species is located at around Mean High Water of Neap Tides (MHWN) (Balke et al., 2016). European salt marsh plant communities follow a clear elevational gradient with the pioneer zone, the lower saltmarsh zone and the upper saltmarsh zone (see Petersen et al., 2014). Salt marsh plants at low elevations are dominated by flooding and salt tolerant species with little competitive capacity whereas communities of the high salt marsh zone are dominated by less stress tolerant species with higher competitive strength (Armstrong et al., 1985; Minden et al., 2012; Snow and Vince, 1984). This has been confirmed by transplanting experiments (Bertness and Ellison, 1987; Crain et al., 2004;

Pennings et al., 2005). It is currently unknown how fragmentation and potential dispersal limitation would affect species sorting along an elevational gradient whereas dispersal effects have been shown to interact with post dispersal filters (e.g. habitat suitability) to determine plant community assembly in salt marshes (Rand, 2000).

Experimental in situ approaches to metacommunity research require direct or indirect control of dispersal rates and environmental conditions while maintaining full exposure to environmental stochasticity and disturbance. Salt marsh communities with their environmental species sorting are ideal study systems but in situ metacommunity experiments are so far lacking due to the high costs and technical difficulties of creating isolated and replicable salt marsh habitat patches on the tidal flat. With the present study we demonstrate the first in situ metacommunity experiment using salt marsh islands as a model system. Twelve experimental salt marsh islands were constructed at the mesotidal Wadden Sea coast of Germany and were either planted with salt marsh vegetation or kept bare for primary colonisation. In addition to the experimental islands, areas within the salt marsh were stripped off their existing vegetation cover and kept bare or planted with vegetation from lower or higher elevations. This allows the comparison of assembly and disassembly of communities in direct vicinity to their source population compared to a more isolated island location. We hypothesize that the increased flooding and salinity stress will lead to relatively rapid extinction of plant species transplanted from higher elevations to the pioneer zone. The salt marsh plants transplanted to the upper salt marsh elevations are however expected to disappear more slowly and only after the arrival of superior competitors. This process is expected to be delayed even further on the islands with limited arrival and establishment of competitors whereas the associated time scales are currently unknown.

Our experiment aims to answer three main questions: (1) How strongly does the assembly of isolated salt marsh communities differ from the assembly of communities assembled directly neighbouring existing habitats? (2) How quickly do resident species recede when environmental stress increases or superior competitors establish? (3) How strong are new colonisers affected by already present occupants? With this paper we provide the first results of the immediate plant community changes after one year.

2. Methods

2.1. Location

A series of 12 experimental islands were set up in September 2014 on the back-barrier tidal flat of Spiekeroog Island in the German East Frisian Wadden Sea (E 7°43′30″, N 53°45′31″; Fig. 1). The Spiekeroog back barrier tidal flats have a mean tidal range of 2.7 m and are predominantly sandy. A nearby permanent monitoring platform records hydrographic and biogeochemical parameters (Reuter et al., 2009) and a tide gauge is operated by WSA-Emden (Wasserstrassen-und Schifffahrtsamt Emden) (Fig. 1B).

2.2. Experimental design

The experiment consists of two treatments (transplanted and bare) across salt marsh enclosed and experimental island plots with six replicates for each of three elevational zones. Each island is a one treatment only replicate with three levels. Each level is situated at the same elevation as the zones of the nearby salt marsh: pioneer zone (Pio), lower salt marsh (Low), upper salt marsh (Upp). The salt marsh enclosed plots are located on the Island of Spiekeroog North

of the experimental islands (Fig. 1C). To study the changes in existing plant communities, one set of plots were filled with transplanted sods of the lower salt marsh zone taken from the salt marsh nearby ('transplanted treatment', experimental islands and plots with odd numbers Fig. 1C and D, Fig. 2). The bare treatment consists of islands and salt marsh enclosed plots filled with the sediment from the tidal flat (plots with even numbers Fig. 1C). All existing vegetation was removed from the salt marsh enclosed plots prior to filling the plots with tidal flat sediment. Six reference plots in each salt marsh zone located between the manipulated plots were designated to serve as an undisturbed control in addition to the manipulated plots (Fig. 1D). Each replicate plot is 2 × 2 m in size. To avoid potential negative impacts of destructive survey techniques, two subplots of 1 × 1 m were randomly allocated for non-destructive surveys (i.e. vegetation surveys, seedling counts etc.) and two subplots of 1 × 1 m were allocated for destructive surveys (e.g. sediment coring etc.).

2.3. Experimental islands

All 12 experimental islands were positioned at the same elevation between 80 and 85 cm NHN (NHN = standard elevation zero) and stretch out over 810 m from NW to SE on the tidal flat (Fig. 1C). The distance between the experimental islands and the salt marsh on Spiekeroog varies between 240 m in the West and 460 m in the East as the tidal flat profile steepens from East to West. The experimental islands are located between 60 m and 120 m apart from each other, as they had to be placed in between the shallow tidal creeks which run from NE to SW. The experimental islands were oriented parallel to these channels with the lower elevational levels facing the island of Spiekeroog.

Each of the 12 islands is made of 12 steel cages (5 mm thick hot-dip galvanised steel) with 4 cages per elevational level (dimensions of each cage = 100 cm × 100 cm x height of pioneer level: 70 cm, lower salt marsh level: 100 cm and upper salt marsh level: 130 cm). These cages were assembled on site into a 2 m × 6 m large island (Fig. 3A). The height of the cages minus 10 cm corresponds to the elevation of the salt marsh plots. Each cage is lined vertically with a geotextile (Huesker HaTe A 1000) fixed at the top of the cage and two polyethylene (PE) bags with 0.14 mm thickness fixed at 50 cm for shorter, 70 cm for intermediate and 80 cm for taller cages. The PE bags retain the soil water with groundwater levels typical for nearby salt marshes. The geotextile allows the soil water above the upper border of the PE bags to drain through the cage. The cages were filled manually with sediment from the surrounding tidal flat, moving 144 m³ sediment. Each island has a set of reflexed steel shields on top of the cages to protect the sediment from wave scouring during inundation (Fig. 3C). Six islands were filled up to 10 cm below the top of each cage to create bare islands (Fig. 3D). Six islands were additionally planted with sods from the lower salt marsh on top of the tidal flat sediment (Fig. 3E). The shields are perforated at the sides and placed with a gap of 10 cm at the front of each elevational step (see Fig. 3C) to allow import and export of small drift material. To protect the islands from scouring at their base, all islands are placed in the centre of an 8 m × 12 m geotextile (Huesker HaTe®- E 1200 C) joined with hot-dip galvanised steel gratings. The cages were secured with the steel gratings which were in turn secured with earth anchors (Duckbill 68) inserted >1 m deep in the tidal flat around their edges.

2.4. Salt marsh plots

The salt marsh plots are mirroring the treatments on the experimental islands but are enclosed by a potential source population. They were established on a stretch of 90 m from NW to SE
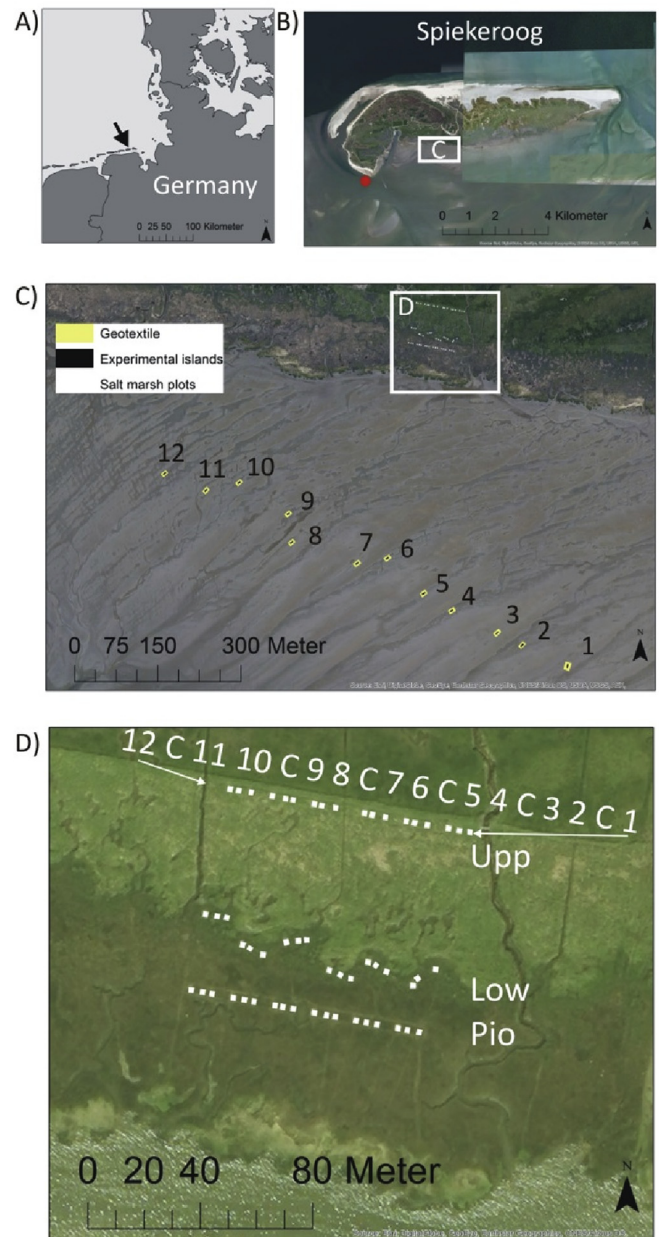

Fig. 1. The Wadden Sea coast of Germany (A) and the Island of Spiekeroog (B). The red marker indicates the location of the tide gauge and permanent monitoring station. The location of the experimental islands and their geotextile foundation on the tidal flat (C) and the salt marsh enclosed plots in the Pioneer zone (Pio), Lower Salt Marsh zone (Low) and Upper Salt Marsh zone (Upp) (D). The numbering in the salt marsh is repeated for each zone (Upp, Low, Pio) from East to West similar to the islands. Transplanted treatments in the salt marsh and on the experimental islands are marked by odd numbers and bare treatments by even numbers. Six control plots (marked as C) per zone are located between the manipulated salt marsh plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 1D). Plots of 2 m × 2 m were marked with bamboo poles in the salt marsh. The vegetation was removed in the bare and transplanted plots to a depth of 30 cm and either filled with sandy tidal flat sediment or approximately 20 × 20 × 30 cm sods of lower salt marsh vegetation according to the assigned treatment. The outside border of each plot was lined with permeable root barrier with 50 g/m² strength to a depth of 30 cm to avoid vegetative colonisation of the plots. The control plots remained untouched.

Elevation	Salt marsh	Salt marsh enclosed		Experimental islands	
	Reference	**Transplanted**	**Bare**	**Transplanted**	**Bare**
Upper salt marsh	Upper	Lower	Bare	Lower	Bare
Lower salt marsh	Lower	Lower	Bare	Lower	Bare
Pioneer salt marsh	Pioneer	Lower	Bare	Lower	Bare

Fig. 2. Experimental design with three elevations (i.e. salt marsh zones) across experimental islands and salt marsh enclosed plots. Each treatment is replicated six times. The plots were either filled with sediment (bare, even numbers in Fig. 1), transplanted with sods from lower salt marsh areas nearby (transplanted, odd numbers in Fig. 1) or left untouched as control treatment (reference). 'Upper', 'Lower', 'Pioneer' and 'Bare' refer to the present vegetation type at the start of the experiment.
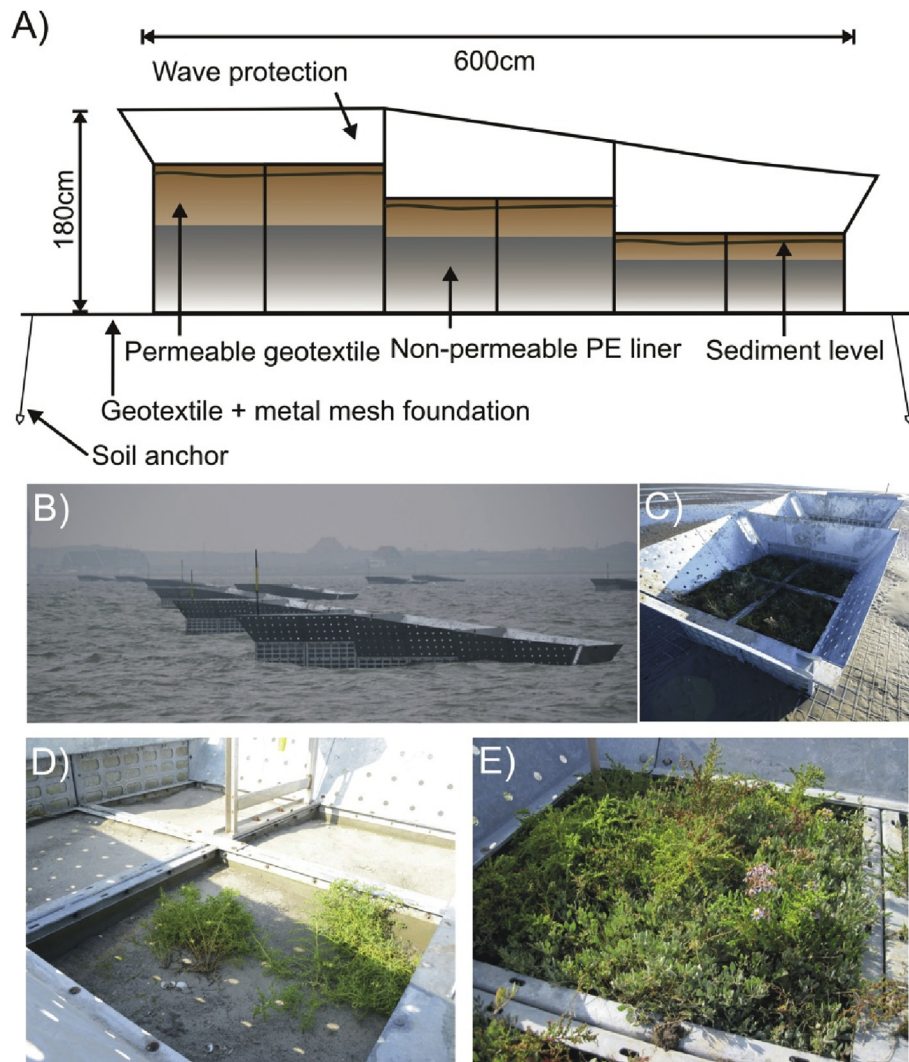

Fig. 3. A) The design of the experimental islands with plastic liners to retain groundwater levels and geotextile to retain the sediment within the islands. The foundation of the islands is made up of a geotextile and metal gratings secured with soil anchors. B) Experimental islands at high tide. C) Experimental island at low tide. D) Initially bare island after one year D) Transplanted lower salt marsh vegetation on an experimental island.

2.5. Abiotic monitoring

Six HOBO® U20L Water Level Logger (onset® HOBO® Data Loggers, Bourne/MA/USA) were deployed in dip wells within the island and salt marsh plots at each elevation to measure groundwater level and flooding. In total six DEFI-T temperature logger (JFE Advantech Co., Ltd., Tokyo/Japan) were installed at the sediment surface at island and salt marsh plots at all elevations. An RBR*duo* TD | wave sensor (RBR Ltd., Ontario/Canada) was installed on the tidal flat and its elevation was determined relative to each island using a Differential GPS. The wave sensors measured in 10 min intervals with 1024 samples per burst at a 3 Hz sampling rate.

Surface elevation change (i.e. sedimentation − erosion) on top of the sediment within the island plots was measured from the top of the cage, measuring the minimum and maximum distance from the sediment surface. A marker plate was buried in each bare salt marsh plot at approximately 30 cm depth and marked with four 1 mm thick wires at the edges. A 3 mm diameter metal rod was inserted in the sediment to repeatedly record the distance from the sediment surface to the plate at five fixed locations for each plate. Elevation change was then averaged over the five points. Surface elevation change is therefore measured in relation to the bottom of the experimental island or in relation to the marker plate in the salt marsh plots.

2.6. Vegetation survey and data analysis

Vegetation was surveyed for two squares of 1×1 m within the 2×2 m experimental plots that were randomly assigned at the start of the experiment for permanent non-destructive surveys. Plant species presence/absence was recorded for each 10×10 cm area within 0.9×0.9 m quadrants placed at the centre of the plot, for a total of 486 areas in 6 replicates. Plant surveys were conducted directly after installing the experiment in September 2014 and after one year in September 2015. Additional repeated surveys were carried out for *Salicornia* spp. in all bare salt marsh enclosed plots. Monthly photographs were taken with a digital SLR camera between April and August 2015. All *Salicornia* spp. individuals were individually marked and counted from the photographs. On 14th of July and 14th of August the heights of all *Salicornia* spp. individuals were measured in both non-destructively sampled subplots of plot number 12 of each salt marsh zone (Fig. 1D) as pattern were consistent across plots at the same elevation.

For the statistical analysis, we have chosen seven species that are characteristic for the different zones: *Salicornia* spp., *Suaeda maritima* and *Spartina anglica* for the pioneer zone, *Limonium vulgare*, *Atriplex portulacoides* and *Puccinellia maritima* for the lower salt marsh zone and *Elytrigia atherica* for the upper salt marsh zone. Change in species frequency of the transplanted treatments between 2014 and 2015 was analysed using linear mixed-effects models in the *lme4* package (Bates et al., 2015) in the R environment (R Core Team, 2016). A separate model was built for each species except for *E. atherica* as it only occurred in transplanted plots of the upper saltmarsh in 2015. The difference in percentage species presence between 2014 and 2015 was used as the response variable. Location type (i.e. experimental island or salt marsh enclosed), elevation and their interaction term were entered into the model as fixed effects. Intercepts for experimental units were added as random effects to account for a grouped experimental design. Inspection of residuals indicated heteroscedasticity in location type or elevation for some species. In those cases, dummy variables were used to assign the variability to the random effects in the different location types or in different elevation levels. Finally, the Akaike Information Criterion (AIC) was used to select the best model. 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. Least square means and contrast between location type and elevation were calculated with *lsmeans* function in the *lsmeans* package (Searle et al., 1980).

3. Results

3.1. Abiotic monitoring

Flooding duration and frequency decreased with elevation of the different vegetation zones as calculated for each elevation from the water level sensor (Table S1). Overall duration of inundation was higher in winter (September−March) than in summer (March−September). During winter high water extremes, the entire island construction including the wave protection plates was inundated by up to 1 m above the top whereas during very low high water levels even the bottom of the island remained dry (Fig. 4).

Maximum wave height exceeded 2 m near the experimental islands in January 2015 during the storms 'Elon and Felix' (Fig. S2a). Maximum wave height during regular winter storms exceeded 1 m. The sediment within the bare islands was eroded to around 20 cm below the edge of the cages (i.e. 10 cm below the desired elevation) with the upper salt marsh levels being affected the most (Fig. S2b).
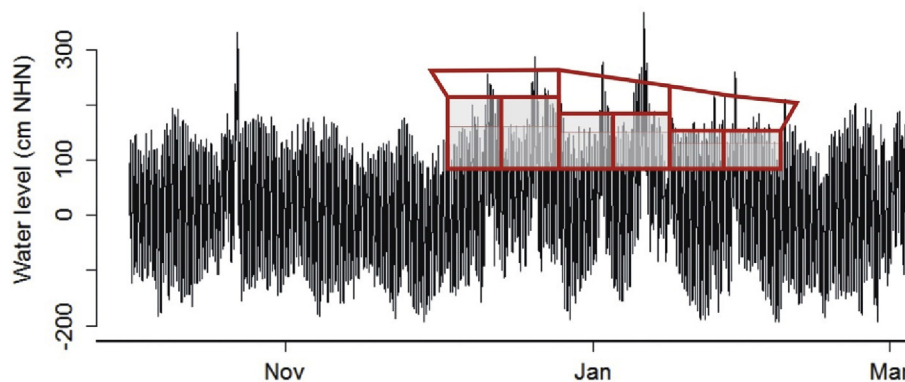

Fig. 4. Tidal water levels at Spiekeroog tide gauge during the winter of 2014/2015 in relation to height of experimental island with base at 80 cm NHN. Mean high water is located at 140 cm NHN and mean low water at −129 cm NHN.

The storms Elon/Felix in January 2015 led to scouring down to the level of the PE bags in all bare islands. The bare island plots were then manually re-filled with tidal flat sediments in January 2015 and the sediment level remained stable during the summer. Variations in surface elevation in the bare salt marsh plots remained between −1 and +1 cm during the winter storms (Fig. S2c).

The temperature on the experimental islands generally matched the temperature within the salt marsh with less than 3 °C difference during extremes (Fig. S3). The temperature fell below zero only on the experimental islands, which occurred four times in the winter 2014/15 but not within the salt marsh enclosed plots.

3.2. Change of plant communities

The surveys of the control plots within the salt marsh correspond with the natural community composition, with *Salicornia* spp. and *Spartina anglica* dominating the pioneer zone, *Atriplex portulacoides*, *Limonium vulgare* and *Puccinellia maritima* dominating the lower salt marsh zone and a monospecific stand of *Elytrigia atherica* in the upper salt marsh zone (Fig. S4). The annual species *Suaeda maritima* occurred both in the pioneer zone and the lower salt marsh zone, although it was more frequent in the latter. Abundance of the annual species *S. maritima* increased in the lower salt marsh zone whereas abundance of *Salicornia* spp. increased in the pioneer zone between 2014 and 2015 (Fig. S4, Table S5).

After one year of development on the initially bare islands, the pioneer zone level was colonised by *Salicornia* spp., *S. maritima* and *P. maritima*, however not exceeding 0.2% presence per species (Fig. 5). The lower salt marsh levels were only colonised by *Salicornia* and *S. maritima* not exceeding 0.6% presence per species, whereas the upper salt marsh levels remained bare. The initially bare salt marsh enclosed plots in the pioneer zone only lacked *A. portulacoides* and *L. vulgare* compared to the reference plots (Fig. 5). In the lower salt marsh zone, only *A. portulacoides* was missing (Fig. 5). The upper salt marsh plots were colonised by all selected species, except *S. anglica*. Perennials did not exceed 6% presence in any zone (Fig. 5). *Salicornia* spp. had colonised all levels of the bare salt marsh enclosed plots with highest densities in the lower salt marsh zone.

The survey of the transplanted sods showed that after one year, *Salicornia* spp. exhibited a significantly higher increase in presence in the salt marsh enclosed plots when compared to the experimental island plots for all zones (P < 0.05). *S. maritima* presence increased on the islands and within the salt marsh in all zones apart from the salt marsh enclosed pioneer zone plot (Fig. 6, Table 1). *Spartina anglica* decreased on the islands, whereas no general trend was observed on the salt marsh plots. *Atriplex portulacoides* decreased in the salt marsh pioneer zone plots where inundation and salinity were higher than in the lower salt marsh zone from where the sods were taken in 2014 (Fig. 6, Table 1). This process was not significant on the experimental islands. *L. vulgare* increased in the lower and upper salt marsh, where the environmental conditions were less harsh. *E. atherica* started to colonise the transplanted communities in the upper salt marsh zone. This happened only in the salt marsh enclosed plots whereas the experimental islands were not colonised by *E. atherica* in the first year.

In the 2014 reference plots species richness was highest in the lower salt marsh zone with a maximum of 10 species, whereas the upper salt marsh had on average less than 2 species and the pioneer salt marsh less than 6 species (Fig. S6). On the initially bare plots highest species richness was observed in the upper salt marsh zone compared to the lower elevations (Fig. S6).

The average number of individuals of the most successful coloniser *Salicornia* spp. across the six bare salt marsh plots showed a similar temporal pattern throughout the year across the three salt marsh zones (Fig. 7a-c). Whereas the average number of individuals increased between April and early July, mortality exceeds new establishment from July towards the end of August (Fig. 7). However, the end of August survey in the pioneer zone showed a small increase in the average number of individuals (Fig. 7a). The highest numbers of individuals were found in the lower salt marsh zone whereas the lowest number was found in the upper salt marsh zone. Tallest individuals were found in the upper salt marsh with no seedling smaller than 10 cm in July and August whereas smaller seedlings of up to 10 cm were dominant in July in the lower salt marsh and pioneer zone with larger individuals of >15 cm only increasing in number in August.

4. Discussion

After one year the experiment provided valuable insights on what metacommunity processes have immediate effects on vegetation population. The bare experimental islands were colonised after one year despite severe erosion during a January storm. Pioneer species with high fecundity (*Salicornia* spp. and *S. maritima*) were the main colonisers of the bare plots, also at higher elevations where they usually do not occur due to competitive exclusion. Mortality due to increased inundation stress of transplanted individuals was species specific and it only occurred for some species in the first year. Future community development may be heavily influenced by environmental stochasticity. Overall, the present study demonstrates the suitability of salt marsh islands as a model system for in situ metacommunity experiments.

The experiment allowed the study of the relationships between niche realisation and isolation of patches in the assembly of spatially structured communities (i.e. along an environmental gradient). Our results are in line with the predictions that at the upper zone of tidal influence, plant niche limits are set by competition rather than stress where few species dominate the community (Bertness and Ellison, 1987; Crain et al., 2004; Pennings et al., 2005). We show that at the seaward limit only few species can tolerate high salinities and flooding even in the absence of competition. This leads to a hump-shaped species richness along an elevational gradient with a maximum at intermediate elevations as it is evident from the control plots of our experiment (Fig. 6 and Fig. S7). On the bare plots however, where competition was absent in the first year, more species colonised the bare upper salt marsh enclosed plots than the lower elevation plots (Fig. S7). *Salicornia* spp., a typical pioneer species which is usually outcompeted at higher elevations, was the most successful coloniser of the bare upper salt marsh plots. *L. vulgare*, *A. portulacoides* and *E. atherica* were still absent from the bare pioneer plots, a clear indication of species sorting due to environmental stress (Fig. 5). Within a metacommunity it is expected that species richness and density increase with increasing habitat connectivity until a superior competitor eventually enters the community and displaces less competitive species (Horn and MacArthur, 1972; Tilman, 1994). The time scales of such competitive displacement with respect to distance from source populations are poorly studied but likely to take several years for *E. atherica* in salt marshes (Rozema et al., 2000; Bakker et al., 2005). In our experiment *E. atherica* was still absent from the experimental islands after one year but colonised the salt marsh enclosed plots of the upper salt marsh although at low frequencies. The competitive effect of *E. atherica* is mainly due to its
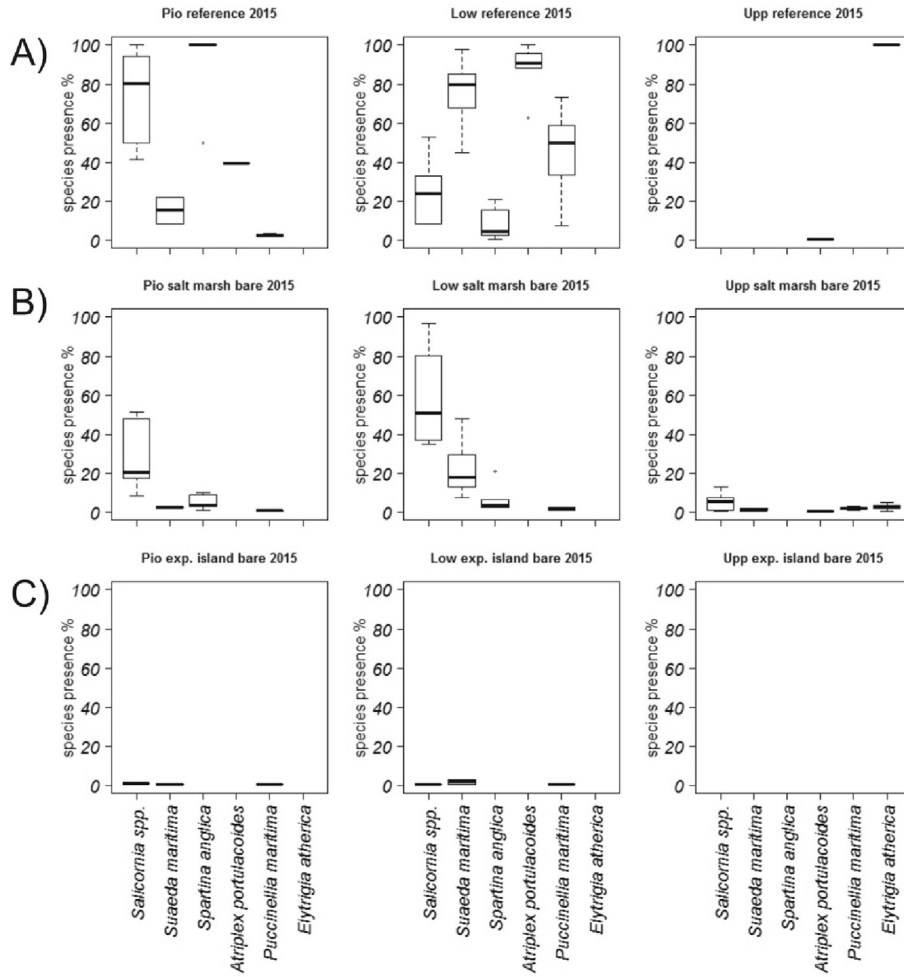
Fig. 5. Species presence in 2015 in reference plots (A) initially bare salt marsh enclosed plots (B) and on bare experimental islands (C). Pio: pioneer zone, Low: lower salt marsh zone, Upp: upper salt marsh zone.
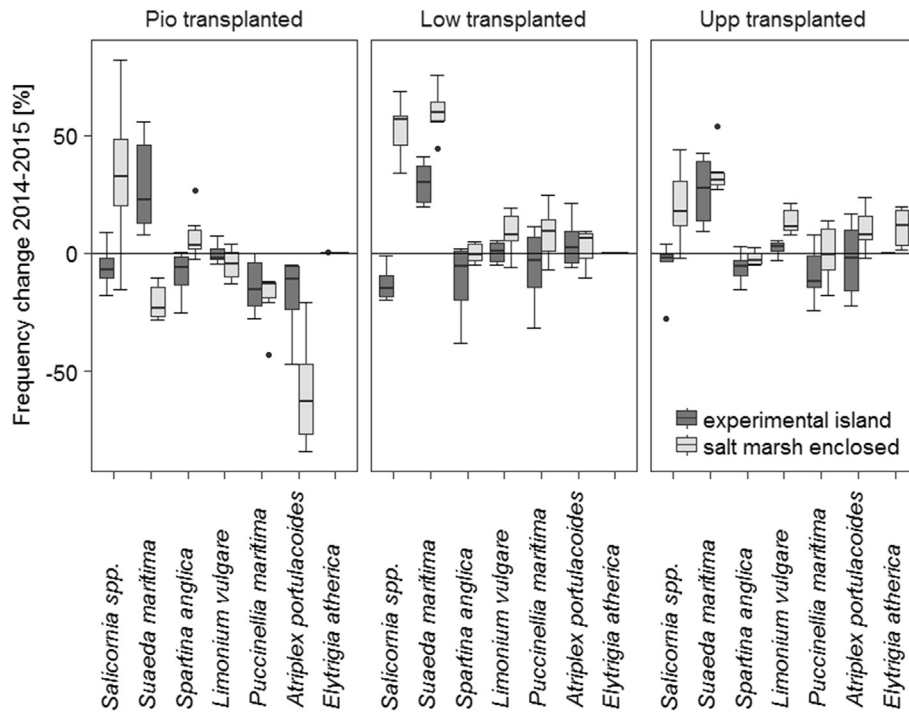
Fig. 6. Frequency change for seven selected species between 2014 and 2015 in transplanted treatments on the experimental islands and salt marsh enclosed plots.

dense, persistent litter layer with a high tissue C:N ratio (Grace and Pugesek, 1997; Minden and Kleyer, 2011). Competitive displacement of other species has not been observed but will be monitored throughout the coming years to quantify the time span and trajectory of community assembly in initially bare plots both isolated and non-isolated.

With accelerated sea-level rise, salt marsh communities may drown if sediment accretion cannot keep up with rising sea levels (Kirwan et al., 2016). This can lead to a displacement of species along the elevational gradient. The species of the drowning marsh may thus create priority effects which may alter establishment conditions for the displaced species (Körner et al., 2008; Louette et al., 2008). This has not been studied in a metacommunity context before but is highly relevant in times of accelerated sea level rise. Transplanted sods of lower salt marsh vegetation into the pioneer zone already showed that *Atriplex portulacoides* and *Puccinellia maritima* rapidly died due to increased flooding (Fig. 6). This effect however was less dominant on the islands. This result may be attributed to artificially kept, constant ground water levels and hence rapid drainage of the upper sediment layers on the islands after flooding on the islands. Priority effects such as the delayed colonisation by *Elytrigia atherica* of the transplanted plots compared to the bare plots in the upper salt marsh or *Spartina anglica* in the pioneer zone were not detected. Both species only reached very low presence in both treatments. Our results therefore confirm that local extinctions due to competition or fragmentation can take considerably more time than those due to stress (Cousins, 2006; Helm et al., 2005; Lindborg and Eriksson, 2004).

The bare salt marsh plots filled with tidal flat sediment allowed high frequency observations of population dynamics along an environmental gradient. Colonisation by *Salicornia* spp. showed similar temporal pattern of seedling emergence and mortality across elevational zones as observed in a natural saltmarsh by

Jefferies et al. (1981). The overall smaller number of individuals in the upper salt marsh may primarily be attributed to reduced inundation events and hence overall reduced seed deposition in the first year compared to lower elevations (Wolters et al., 2004) and to the lack of short-distance seed supply due to absence of *Salicornia* spp. in the upper salt marsh community (Rand, 2000). Limited water storage capacity of the sandy tidal flat sediments in the bare upper salt marsh and island plots may also have created unsuitable soil moisture and salinity conditions during periods of germination. Growth conditions for established plants however seemed more suitable in the upper salt marsh (i.e. larger size of individuals). These observations highlight the relatively small-scale differences in population dynamics of *Salicornia* spp. The relative importance of seed deposition versus seedling emergence and mortality requires further investigation for all *Salicornia* species and subspecies to fully explain the effects of the environmental gradient.

Overall the monitoring data suggests that the experimental islands are not only more isolated from the source population but also more exposed to wave attack and temperature minima during winter. This has to be considered for future analyses of the community development and will be met with frequent monitoring of abiotic parameters. The sediment within the bare islands was eroded by wave scouring down to the artificial groundwater level of all six bare islands during a major storm event with 2 m wave height around the islands (Elon/Felix winter storm in January 2015). We addressed this by installing polycarbonate covers directly on top of each 1 × 1 m cage during the following stormy season between October and March (Fig. S7). The perforated covers allow gas, water and seed exchange and successfully reduced scouring during the storm season of 2015/16. Although physical disturbance is part of the dynamics of salt marsh habitats, we acknowledge that this severe erosion may have led to limited colonisation success of the bare islands in the first year as potentially deposited seeds during the autumn may have been eroded
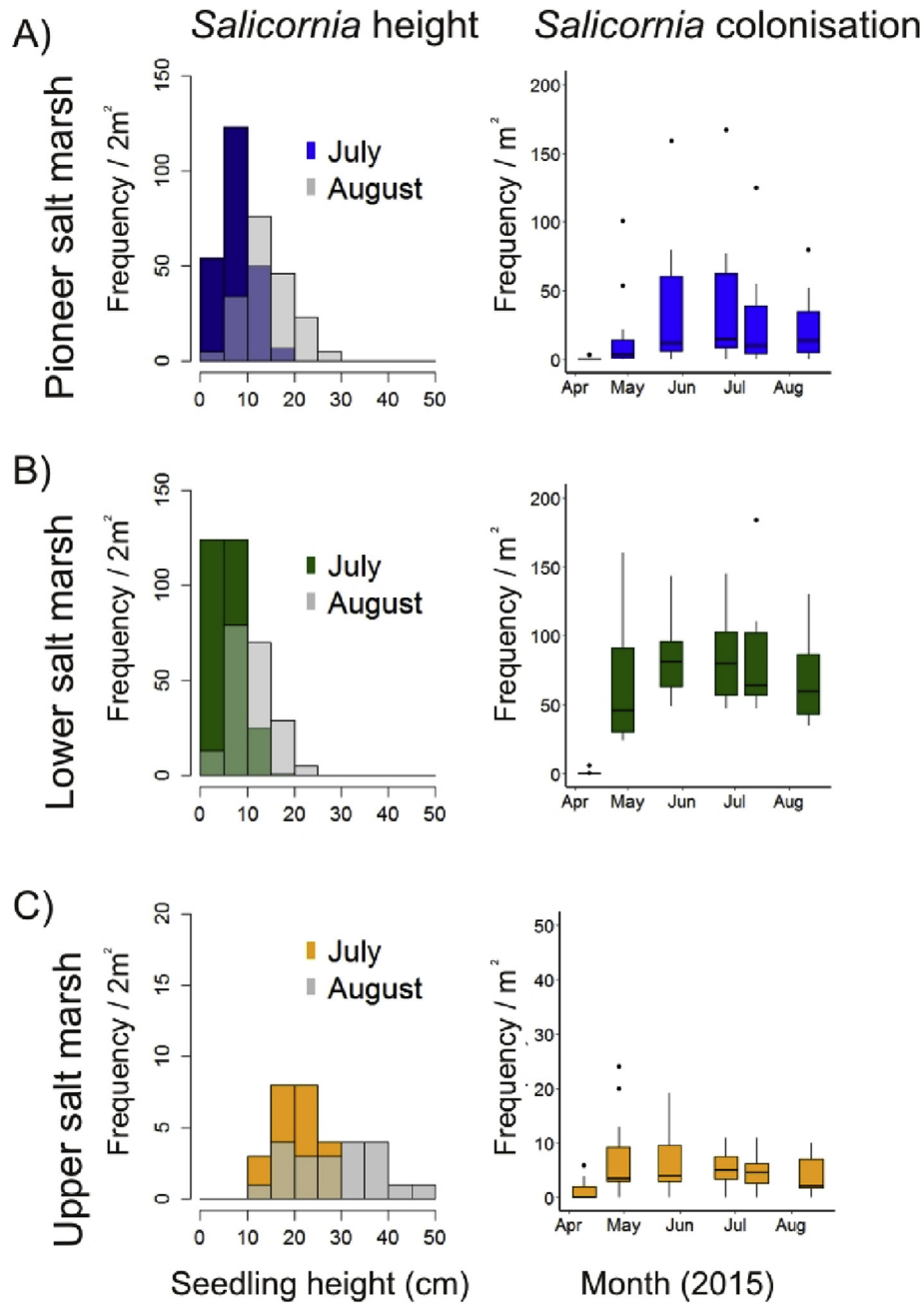
Fig. 7. Height histogram of all *Salicornia* spp. individuals in the bare salt marsh enclosed plot No 12 on 13th July and 13th August 2015 (panel on the left). Boxplot of monthly count data of *Salicornia* spp. individuals in all bare salt marsh plots (panel on the right). Note that y axis has been clipped at 200 in A) and B) not showing all extreme values of the boxplot.

Table 1
Changes in species presence between 2014 and 2015. Least square means and standard errors from linear mixed-effect models. Bold values are significant changes based on 95% confidence intervals. For *Puccinellia* only elevation and for *Spartina* only plot type was considered for fixed effects.

	Salt marsh enclosed plots						Experimental islands						R^2 marginal	R^2 conditional
	Pio		Low		Upp		Pio		Low		Upp			
Salicornia	**33.6**	7.3	**52.9**	7.3	**20.3**	7.3	−5.9	6.7	−12.9	6.7	−5.3	6.7	0.66	0.69
Suaeda	**−20.7**	5.3	**59.9**	5.3	**34.5**	5.3	**28.7**	5.3	**29.7**	5.3	**26.4**	5.3	0.78	0.87
Atriplex	**−58.8**	8.1	2.6	4.6	10.2	5.3	−17.6	8.1	4.2	4.6	−2.8	5.3	0.71	0.85
Limonium	−4.7	2.4	**8.6**	2.4	**13.5**	2.4	−0.1	2.4	0.4	2.4	2.4	2.4	0.51	0.51
Puccinellia	**−16.4**	3.9	1.4	3.9	−4.3	3.9							0.24	0.27
Spartina			1.7	2.2					**−8.7**	2.2			0.25	0.27

during the January storm. The experiment demonstrated however that unassisted dispersal to the islands was generally possible after one season with a clear selection for early successional species such as *Salicornia* spp. and *S. maritima*. Species-specific differences of early colonisation success is an important criterion for the patch dynamics paradigm in metacommunity ecology (Kneitel and Chase, 2004; Winegardner et al., 2012).

5. Conclusion

The first year of this longer-term experiment supports existing theory. Species sorting was evident as transplanted vegetation developed differently in the three elevational salt marsh zones. As expected, early colonising species such as *Salicornia* spp. dominated the initially bare salt marsh enclosed plots across elevations but species number was highest in the least often inundated upper salt marsh plots in the absence of competition. Limited colonisation of the bare experimental islands may have been attributed to severe sediment erosion in January but generally showed that unassisted colonisation was possible. Differences in colonisation success of bare patches by *Salicornia* spp. were not only observed between island and salt marsh plots but also between elevational zones within the marsh. The relevance of mass effects (Leibold et al., 2004; Turnbull et al., 2004) (i.e. effect of immigration from larger source populations) may only be observed over longer timescales with increasing competitive exclusion by new arrivals on the plots. Comparing the future assemblies on the transplanted plots with the bare plots will allow to address potential priority effects (i.e. effects of existing species on new arrivals) and the time scales of local extinctions due to stress versus competition. The exposure to environmental variability and disturbance (such as frost, drought or storm events) is an integral part of this in situ experimental design. However, stochastic disturbance in coastal ecosystems may make vegetation development less predictable when compared to laboratory experiments (Balke et al., 2014). Hence long-term observations will be necessary to account for environmental variability and stochasticity.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2017.09.021.

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