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1 **Experimental salt marsh islands: a model system**

2 **for novel metacommunity experiments**

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23 Abstract:

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

39

40 Keywords: niche, priority effects, dispersal, Wadden Sea, transplants, competition, patch
41 dynamics, species sorting.

42

43

44 **Introduction**

45 Species composition and ecosystem functioning in aquatic and terrestrial ecosystems
46 cannot be understood by studying local processes alone. Local competitive and trophic
47 interactions have to be studied in a metacommunity context as communities on habitat patches
48 that are connected with each other by dispersal (Amarasekare and Nisbet, 2001; Holyoak et al.,
49 2005; Leibold et al., 2004). Metacommunity theory has increasingly gained attention since the
50 1990s (Wilson, 1992) and amends classical ecological theory by acknowledging the spatial
51 dynamics of species and alleviating the assumption that local communities are regulated by
52 local niche processes alone (Hillebrand and Blenckner, 2002; Leibold et al., 2004; Shurin and
53 Allen, 2001). To date few field experiments have tried to investigate its basic principles despite
54 the importance of habitat fragmentation and shifting species ranges with climate change (Logue
55 et al., 2011; Grainger and Gilbert, 2016). Here we present the first year's results of a real scale
56 metacommunity field experiment using salt marsh islands as a model system.

57 Local niche partitioning should dominate community assembly when assuming
58 unlimited dispersal, large population size and stable environmental conditions. This means that
59 in a heterogeneous environment species are not restricted to filling their respective niches
60 (Leibold et al., 2004). Under dispersal limitation however community assembly may be
61 dominated by species with high dispersal ability, especially when competitive species with poor
62 dispersability are not able to fill in their respective niche. Dispersal limitation in a
63 metacommunity may therefore lead to different or delayed assembly sequences compared to
64 situations with unlimited dispersal (Drake, 1991; Fukami et al., 2005) and is thus suggested to
65 affect local biodiversity (Mouquet and Loreau, 2003) and ecosystem properties (Koerner et al.,
66 2008). Environmental change often generates succession where resident (i.e. already present)
67 species are eventually replaced by better adapted colonising species. Species composition at a
68 given time therefore depends on the elapsed time since environmental change occurred, the
69 persistence of the residents and the dispersal and competitive abilities of newly arriving species
70 (Lindborg and Eriksson, 2004). Bare unoccupied patches may get colonised more rapidly by a
71 newly arriving species compared to already occupied patches where priority effects (i.e. earlier
72 presence of a particular species and the effect of species arrival sequences) may prevent
73 subsequent colonisation and establishment (Loeuille and Leibold, 2008). Such usually
74 deterministic changes in species composition may become stochastic when short term
75 variability of the environmental conditions continuously interrupts the directional development

76 of the community. Competitive traits and trait based sorting of species may become secondary
77 in stochastic community assemblies.

78 Modelling has been the predominant tool to explore community assembly in a
79 metacommunity context (Kneitel and Chase, 2004; Mouquet and Loreau, 2002; Shoemaker and
80 Melbourne, 2016) with little empirical evidence (Grainger and Gilbert, 2016; Logue et al.,
81 2011). The majority of metacommunity experiments deal with the disassembly of communities
82 after experimental fragmentation (Haddad et al., 2015), where researchers often observe a slow
83 decline of species richness towards a new equilibrium (Gonzalez, 2000). Only few in situ
84 experiments have studied metacommunity assembly mechanisms exposed to stochasticity of
85 environmental conditions (Mouquet et al., 2004; Resasco et al., 2014).

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

99 The elevational border between tidal flat habitats with predominantly marine organisms
100 and the habitat of terrestrial salt marsh plant species is located at around Mean High Water of
101 Neap Tides (MHWN) (Balke et al., 2016). European salt marsh plant communities follow a
102 clear elevational gradient with the pioneer zone, the lower saltmarsh zone and the upper
103 saltmarsh zone (see Petersen et al., 2014). Salt marsh plants at low elevations are dominated by
104 flooding and salt tolerant species with little competitive capacity whereas communities of the
105 high salt marsh zone are dominated by less stress tolerant species with higher competitive
106 strength (Armstrong et al., 1985; Minden et al., 2012; Snow and Vince, 1984). This has been
107 confirmed by transplanting experiments (Bertness and Ellison, 1987; Crain et al., 2004;
108 Pennings et al., 2005). It is currently unknown how fragmentation and potential dispersal

109 limitation would affect species sorting along an elevational gradient whereas dispersal effects
110 have been shown to interact with post dispersal filters (e.g. habitat suitability) to determine
111 plant community assembly in salt marshes (Rand, 2000)

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

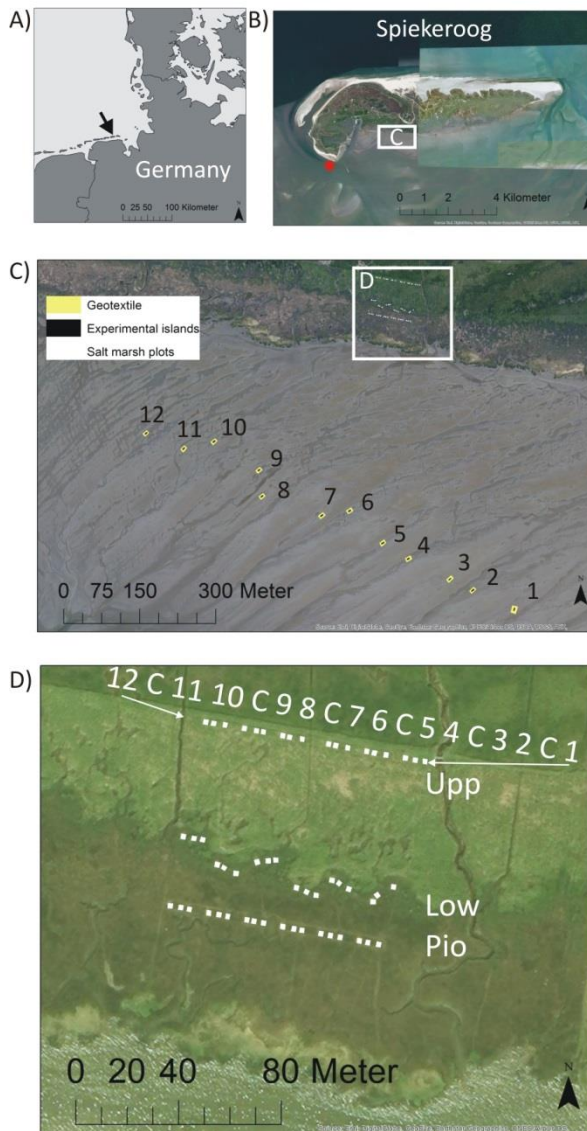
131 Our experiment aims to answer three main questions: (1) How strongly does the
132 assembly of isolated salt marsh communities differ from the assembly of communities
133 assembled directly neighbouring existing habitats? (2) How quickly do resident species recede
134 when environmental stress increases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

137

138 **Methods**

139 *Location*

140 A series of 12 experimental islands were set up in September 2014 on the back-barrier
 141 tidal flat of Spiekeroog Island in the German East Frisian Wadden Sea (E 7°43'30'', N
 142 53°45'31''; Fig. 1). The Spiekeroog back barrier tidal flats have a mean tidal range of 2.7 m
 143 and are predominantly sandy. A nearby permanent monitoring platform records hydrographic
 144 and biogeochemical parameters (Reuter et al., 2009) and a tide gauge is operated by WSA-
 145 Emden (Wasserstrassen- und Schifffahrtsamt Emden) (Fig. 1B).



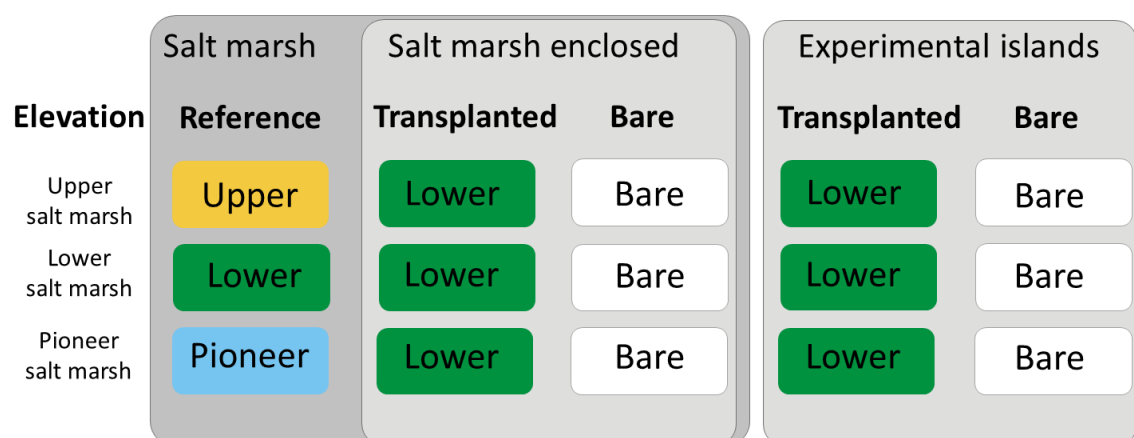
146
 147 Fig. 1. The Wadden Sea coast of Germany (A) and the Island of Spiekeroog (B). The red marker
 148 indicates the location of the tide gauge and permanent monitoring station. The location of the
 149 experimental islands and their geotextile foundation on the tidal flat (C) and the salt marsh
 150 enclosed plots in the Pioneer zone (Pio), Lower Salt Marsh zone (Low) and Upper Salt Marsh
 151 zone (Upp) (D). The numbering in the salt marsh is repeated for each zone (upp, low, pio) from
 152 East to West similar to the islands. Transplanted treatments in the salt marsh and on the

153 experimental islands are marked by odd numbers and bare treatments by even numbers. Six
 154 control plots (marked as C) per zone are located between the manipulated salt marsh plots.

155

156 *Experimental design*

157 The experiment consists of two treatments (transplanted and bare) across salt marsh
 158 enclosed and experimental island plots with six replicates for each of three elevational zones.
 159 Each island is a one treatment only replicate with three levels. Each level is situated at the same
 160 elevation as the zones of the nearby salt marsh: pioneer zone (pio), lower salt marsh (low),
 161 upper salt marsh (upp). The salt marsh enclosed plots are located on the Island of Spiekeroog
 162 North of the experimental islands (Fig. 1C). To study the changes in existing plant communities,
 163 one set of plots were filled with transplanted sods of the lower salt marsh zone taken from the
 164 salt marsh nearby ('transplanted treatment', experimental islands and plots with odd numbers
 165 Fig. 1C and 1D, Fig. 2). The bare treatment consists of islands and salt marsh enclosed plots
 166 filled with the sediment from the tidal flat (plots with even numbers Fig. 1 C). All existing
 167 vegetation was removed from the salt marsh enclosed plots prior to filling the plots with tidal
 168 flat sediment. Six reference plots in each salt marsh zone located between the manipulated plots
 169 were designated to serve as an undisturbed control in addition to the manipulated plots (Fig.
 170 1D). Each replicate plot is 2x2 m in size. To avoid potential negative impacts of destructive
 171 survey techniques, two subplots of 1x1 m were randomly allocated for non-destructive surveys
 172 (i.e. vegetation surveys, seedling counts etc.) and two subplots of 1x1 m were allocated for
 173 destructive surveys (e.g. sediment coring etc.).



174

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

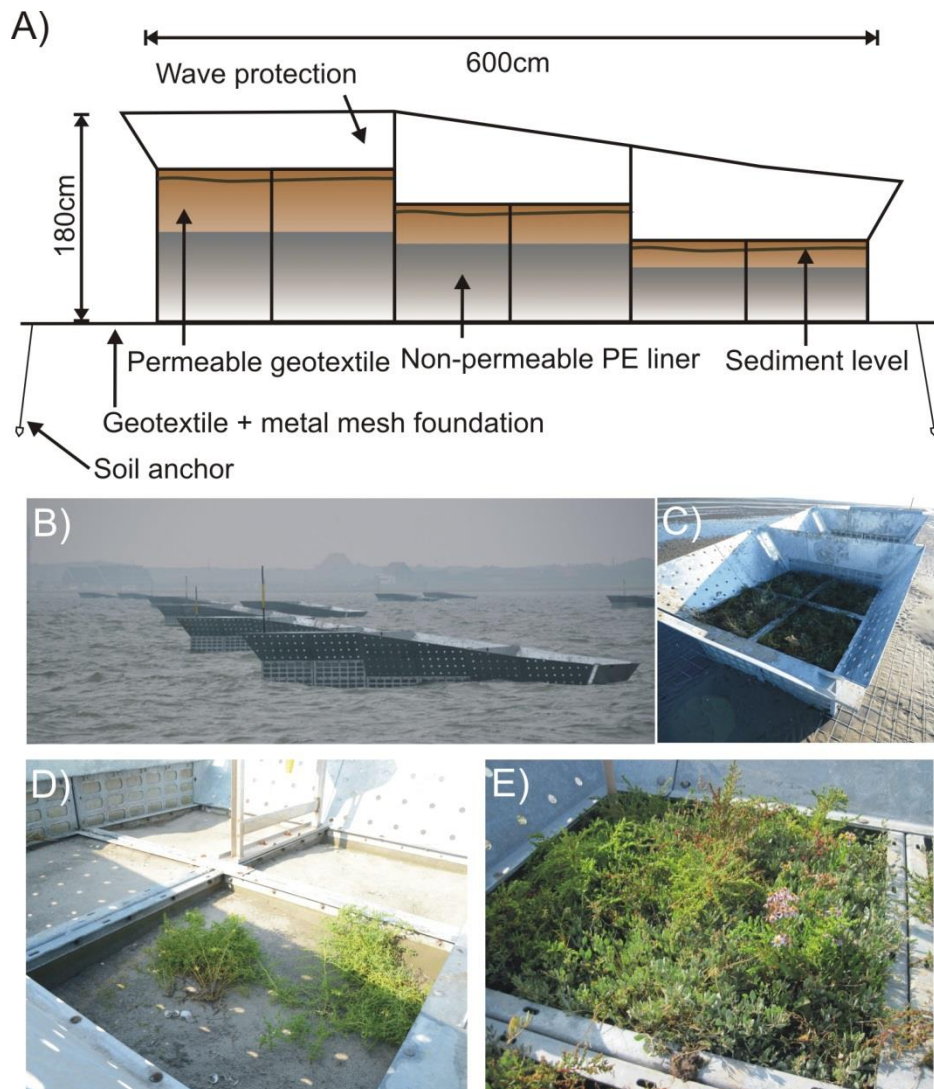
181 *Experimental islands*

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

190 Each of the 12 islands is made of 12 steel cages (5 mm thick hot-dip galvanised steel)
191 with 4 cages per elevational level (dimensions of each cage = 100 cm x 100 cm x height of
192 pioneer level: 70 cm, lower salt marsh level: 100 cm and upper salt marsh level: 130 cm). These
193 cages were assembled on site into a 2 m x 6 m large island (Fig. 3A). The height of the cages
194 minus 10 cm corresponds to the elevation of the salt marsh plots. Each cage is lined vertically
195 with a geotextile (Huesker HaTe A 1000) fixed at the top of the cage and two polyethylene (PE)
196 bags with 0.14 mm thickness fixed at 50 cm for shorter, 70 cm for intermediate and 80 cm for
197 taller cages. The PE bags retain the soil water with groundwater levels typical for nearby salt
198 marshes. The geotextile allows the soil water above the upper border of the PE bags to drain
199 through the cage. The cages were filled manually with sediment from the surrounding tidal flat,
200 moving 144 m³ sediment. Each island has a set of reflexed steel shields on top of the cages to
201 protect the sediment from wave scouring during inundation (Fig. 3C). Six islands were filled
202 up to 10 cm below the top of each cage to create bare islands (Fig. 3D). Six islands were
203 additionally planted with sods from the lower salt marsh on top of the tidal flat sediment (Fig.
204 3E). The shields are perforated at the sides and placed with a gap of 10 cm at the front of each
205 elevational step (see Fig. 3C) to allow import and export of small drift material. To protect the
206 islands from scouring at their base, all islands are placed in the centre of an 8 m x 12 m
207 geotextile (Huesker HaTe®- E 1200 C) joined with hot-dip galvanised steel gratings. The cages

208 were secured with the steel gratings which were in turn secured with earth anchors (Duckbill
209 68) inserted >1 m deep in the tidal flat around their edges.

210



211

212

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

218 *Salt marsh plots*

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

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

227 *Abiotic monitoring*

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

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

244

245 *Vegetation survey and data analysis*

246 Vegetation was surveyed for two squares of 1 x 1 m within the 2 x 2 m experimental
247 plots that were randomly assigned at the start of the experiment for permanent non-destructive
248 surveys. Plant species presence/absence was recorded for each 10 x 10cm area within 0.9 x 0.9
249 m quadrants placed at the centre of the plot, for a total of 486 areas in 6 replicates.. Plant surveys
250 were conducted directly after installing the experiment in September 2014 and after one year in
251 September 2015. Additional repeated surveys were carried out for *Salicornia* spp. in all bare
252 salt marsh enclosed plots. Monthly photographs were taken with a digital SLR camera between

253 April and August 2015. All *Salicornia* spp. individuals were individually marked and counted
254 from the photographs. On 14th of July and 14th of August the heights of all *Salicornia* spp.
255 individuals were measured in both non-destructively sampled subplots of plot number 12 of
256 each salt marsh zone (Fig. 1D) as pattern were consistent across plots at the same elevation.

257

258 For the statistical analysis, we have chosen seven species that are characteristic for the
259 different zones: *Salicornia* spp., *Suaeda maritima* and *Spartina anglica* for the pioneer zone,
260 *Limonium vulgare*, *Atriplex portulacoides* and *Puccinellia maritima* for the lower salt marsh
261 zone and *Elytrigia atherica* for the upper salt marsh zone. Change in species frequency of the
262 transplanted treatments between 2014 and 2015 was analysed using linear mixed-effects models
263 in the *lme4* package (Bates et al., 2015) in the R environment (R Core Team 2016). A separate
264 model was built for each species except for *E. atherica* as it only occurred in transplanted plots
265 of the upper saltmarsh in 2015. The difference in percentage species presence between 2014
266 and 2015 was used as the response variable. Location type (i.e. experimental island or salt marsh
267 enclosed), elevation and their interaction term were entered into the model as fixed effects.
268 Intercepts for experimental units were added as random effects to account for a grouped
269 experimental design. Inspection of residuals indicated heteroscedasticity in location type or
270 elevation for some species. In those cases, dummy variables were used to assign the variability
271 to the random effects in the different location types or in different elevation levels. Finally, the
272 Akaike Information Criterion (AIC) was used to select the best model. Marginal and conditional
273 R^2 following Johnson (2014) were calculated to estimate the model fit. Marginal R^2 for mixed-
274 effect models measures the variance explained by fixed effects, conditional R^2 additionally
275 includes the variance explained by fixed and random effects. Least square means and contrast
276 between location type and elevation were calculated with *lsmeans* function in the *lsmeans*
277 package (Searle et al., 1980).

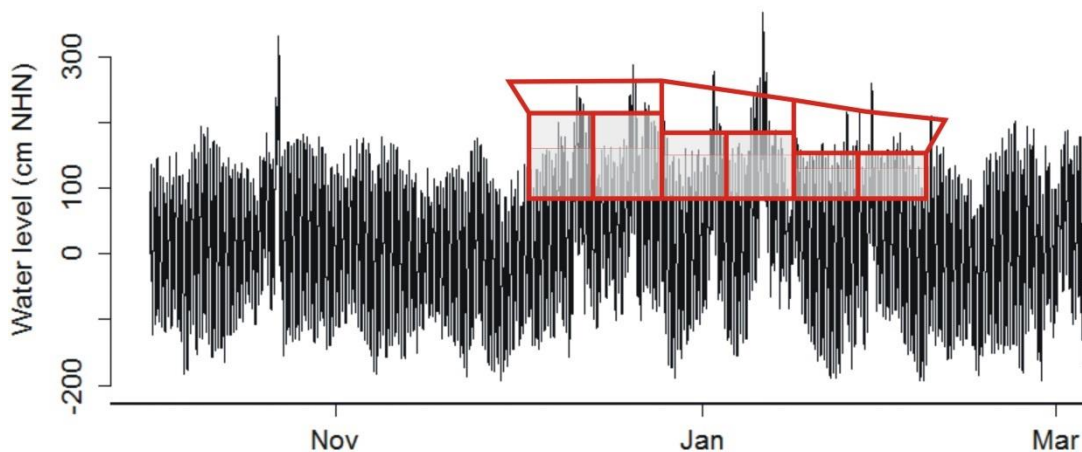
278 **Results**

279 *Abiotic monitoring*

280 Flooding duration and frequency decreased with elevation of the different vegetation
281 zones as calculated for each elevation from the water level sensor (Tab. S1). Overall duration
282 of inundation was higher in winter (September – March) than in summer (March – September).
283 During winter high water extremes, the entire island construction including the wave protection

284 plates was inundated by up to 1 m above the top whereas during very low high water levels
285 even the bottom of the island remained dry (Fig. 4).

286 Maximum wave height exceeded 2 m near the experimental islands in January 2015
287 during the storms 'Elon and Felix' (Fig. S2a). Maximum wave height during regular winter
288 storms exceeded 1 m. The sediment within the bare islands was eroded to around 20 cm below
289 the edge of the cages (i.e. 10 cm below the desired elevation) with the upper salt marsh levels
290 being affected the most (Fig. S2b). The storms Elon/Felix in January 2015 led to scouring down
291 to the level of the PE bags in all bare islands. The bare island plots were then manually re-filled
292 with tidal flat sediments in January 2015 and the sediment level remained stable during the
293 summer. Variations in surface elevation in the bare salt marsh plots remained between -1 and
294 +1 cm during the winter storms (Fig. S2c).



295

296

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

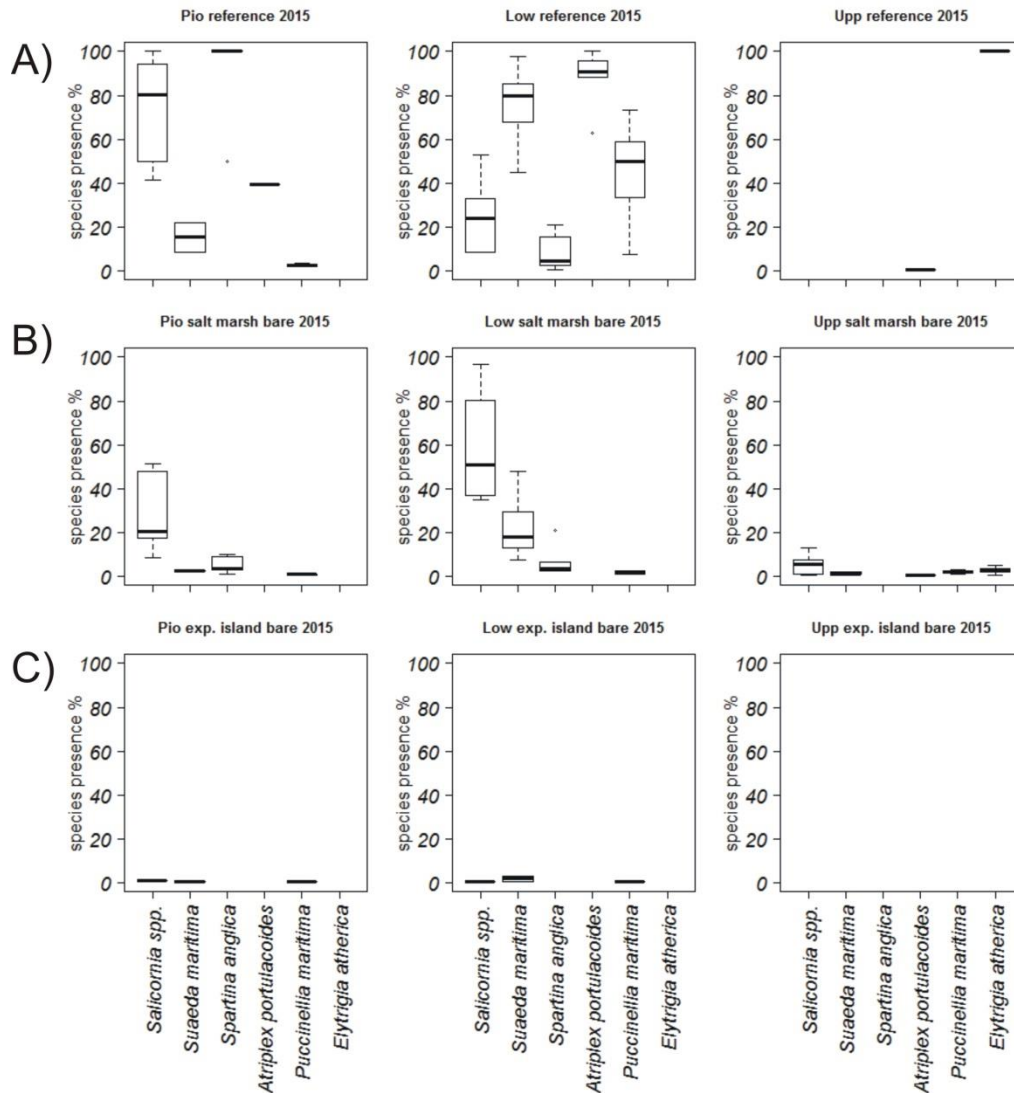
300 The temperature on the experimental islands generally matched the temperature within
301 the salt marsh with less than 3 °C difference during extremes (Fig. S3). The temperature fell
302 below zero only on the experimental islands, which occurred four times in the winter 2014/15
303 but not within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

304

305 *Change of plant communities*

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

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

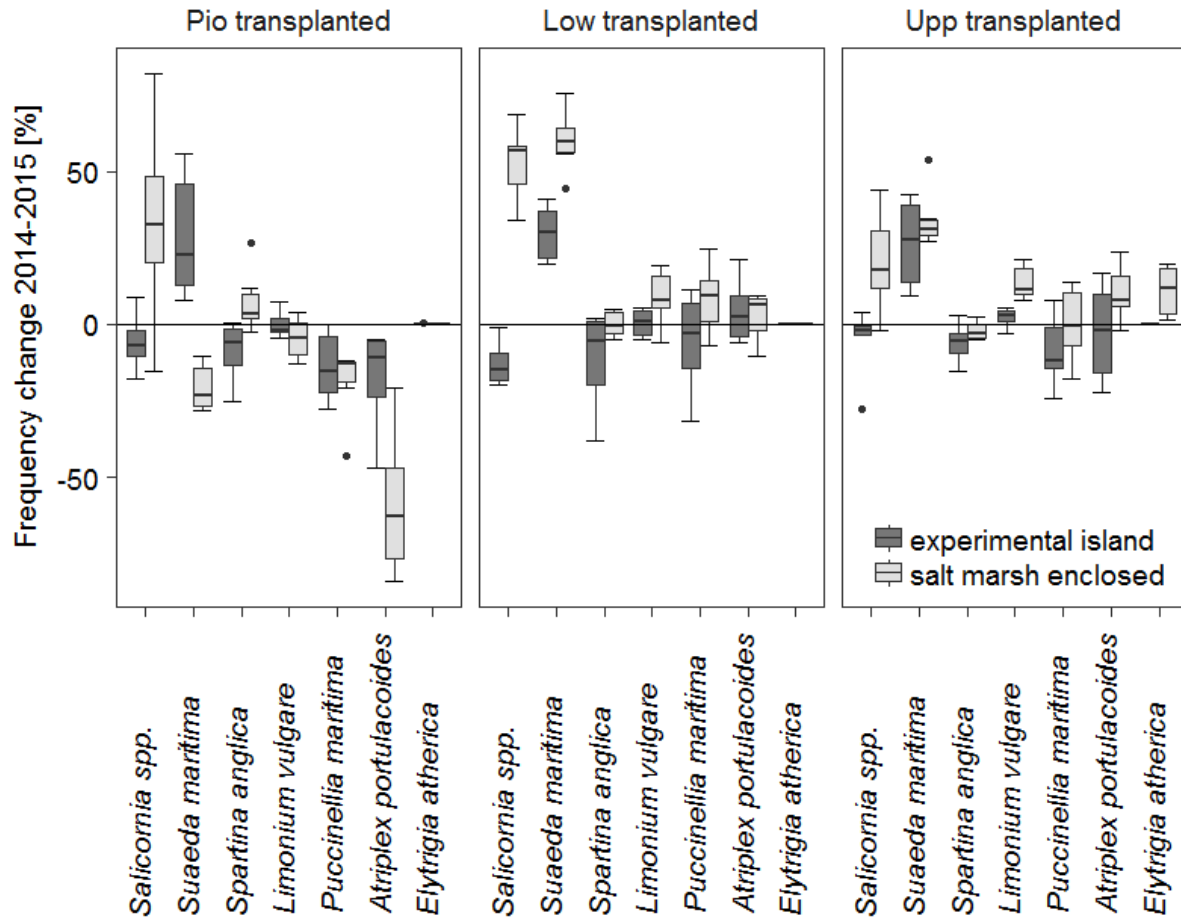


324

325 Fig. 5. Species presence in 2015 in reference plots (A) initially bare salt marsh enclosed
 326 plots (B) and on bare experimental islands (C). Pio: pioneer zone, Low: lower salt marsh zone,
 327 Upp: upper salt marsh zone.

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

338 communities in the upper salt marsh zone. This happened only in the salt marsh enclosed plots
 339 whereas the experimental islands were not colonised by *E. atherica* in the first year.



340
 341 Fig. 6. Frequency change for seven selected species between 2014 and 2015 in transplanted
 342 treatments on the experimental islands and salt marsh enclosed plots.

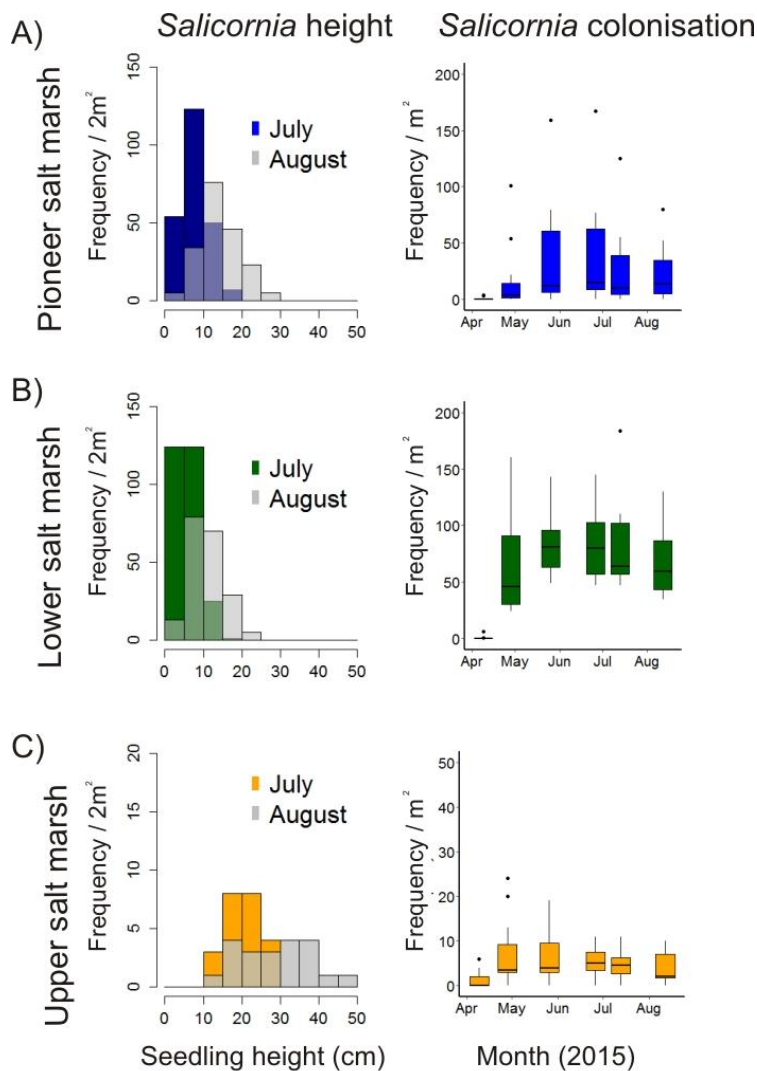
343 Table 1. Changes in species presence between 2014 and 2015. Least square means and standard
 344 errors from linear mixed-effect models. Bold values are significant changes based on 95%
 345 confidence intervals. For *Puccinellia* only elevation and for *Spartina* only plot type was
 346 considered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

	Salt marsh enclosed plots						Experimental islands						R ²	
	pio		low		upp		pio		low		upp		marginal	conditional
<i>Salicornia</i>	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
<i>Suaeda</i>	-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
<i>Atriplex</i>	-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
<i>Limonium</i>	-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
<i>Puccinellia</i>	-16.4	3.9	1.4	3.9	-4.3	3.9							0.24	0.27
<i>Spartina</i>			1.7	2.2					-8.7	2.2			0.25	0.27

347

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

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



364

365 Fig. 7. Height histogram of all *Salicornia* spp. individuals in the bare salt marsh enclosed plot
 366 No 12 on 13th July and 13th August 2015 (panel on the left). Boxplot of monthly count data of
 367 *Salicornia* spp. individuals in all bare salt marsh plots (panel on the right). Note that y axis has
 368 been clipped at 200 in A) and B) not showing all extreme values of the boxplot.

369

370 Discussion

371 After one year the experiment provided valuable insights on what metacommunity
 372 processes have immediate effects on vegetation population. The bare experimental islands were
 373 colonised after one year despite severe erosion during a January storm. Pioneer species with
 374 high fecundity (*Salicornia* spp. and *S. maritima*) were the main colonisers of the bare plots, also
 375 at higher elevations where they usually do not occur due to competitive exclusion. Mortality
 376 due to increased inundation stress of transplanted individuals was species specific and it only
 377 occurred for some species in the first year. Future community development may be heavily

378 influenced by environmental stochasticity. Overall, the present study demonstrates the
379 suitability of salt marsh islands as a model system for in situ metacommunity experiments.

380 The experiment allowed the study of the relationships between niche realisation and
381 isolation of patches in the assembly of spatially structured communities (i.e. along an
382 environmental gradient). Our results are in line with the predictions that at the upper zone of
383 tidal influence, plant niche limits are set by competition rather than stress where few species
384 dominate the community (Bertness and Ellison, 1987; Crain et al., 2004; Pennings et al., 2005).
385 We show that at the seaward limit only few species can tolerate high salinities and flooding
386 even in the absence of competition. This leads to a hump-shaped species richness along an
387 elevational gradient with a maximum at intermediate elevations as it is evident from the control
388 plots of our experiment (Fig. 6, S7). On the bare plots however, where competition was absent
389 in the first year, more species colonised the bare upper salt marsh enclosed plots than the lower
390 elevation plots (Fig. S7). *Salicornia* spp., a typical pioneer species which is usually
391 outcompeted at higher elevations, was the most successful coloniser of the bare upper salt marsh
392 plots. *L. vulgare*, *A. portulacoides* and *E. atherica* were still absent from the bare pioneer plots,
393 a clear indication of species sorting due to environmental stress (Fig. 5). Within a
394 metacommunity it is expected that species richness and density increase with increasing habitat
395 connectivity until a superior competitor eventually enters the community and displaces less
396 competitive species (Horn and MacArthur, 1972; Tilman, 1994). The time scales of such
397 competitive displacement with respect to distance from source populations are poorly studied
398 but likely to take several years for *E. atherica* in salt marshes (Rozema et al., 2000; Bakker et
399 al., 2005). In our experiment *E. atherica* was still absent from the experimental islands after
400 one year but colonised the salt marsh enclosed plots of the upper salt marsh although at low
401 frequencies. The competitive effect of *E. atherica* is mainly due to its dense, persistent litter
402 layer with a high tissue C:N ratio (Grace and Pugsek, 1997; Minden and Kleyer, 2011).
403 Competitive displacement of other species has not been observed but will be monitored
404 throughout the coming years to quantify the time span and trajectory of community assembly
405 in initially bare plots both isolated and non-isolated.

406 With accelerated sea-level rise, salt marsh communities may drown if sediment
407 accretion cannot keep up with rising sea levels (Kirwan et al., 2016). This can lead to a
408 displacement of species along the elevational gradient. The species of the drowning marsh may
409 thus create priority effects which may alter establishment conditions for the displaced species
410 (Körner et al., 2008; Louette et al., 2008). This has not been studied in a metacommunity context

411 before but is highly relevant in times of accelerated sea level rise. Transplanted sods of lower
412 salt marsh vegetation into the pioneer zone already showed that *Atriplex portulacoides* and
413 *Puccinellia maritima* rapidly died due to increased flooding (Fig. 6). This effect however was
414 less dominant on the islands. This result may be attributed to artificially kept, constant ground
415 water levels and hence rapid drainage of the upper sediment layers on the islands after flooding
416 on the islands. Priority effects such as the delayed colonisation by *Elytrigia atherica* of the
417 transplanted plots compared to the bare plots in the upper salt marsh or *Spartina anglica* in the
418 pioneer zone were not detected. Both species only reached very low presence in both treatments.
419 Our results therefore confirm that local extinctions due to competition or fragmentation can
420 take considerably more time than those due to stress (Cousins, 2006; Helm et al., 2005;
421 Lindborg and Eriksson, 2004).

422 The bare salt marsh plots filled with tidal flat sediment allowed high frequency
423 observations of population dynamics along an environmental gradient. Colonisation by
424 *Salicornia* spp. showed similar temporal pattern of seedling emergence and mortality across
425 elevational zones as observed in a natural saltmarsh by Jefferies et al., (1981). The overall
426 smaller number of individuals in the upper salt marsh may primarily be attributed to reduced
427 inundation events and hence overall reduced seed deposition in the first year compared to lower
428 elevations (Wolters et al., 2004) and to the lack of short-distance seed supply due to absence of
429 *Salicornia* spp. in the upper salt marsh community (Rand, 2000). Limited water storage capacity
430 of the sandy tidal flat sediments in the bare upper salt marsh and island plots may also have
431 created unsuitable soil moisture and salinity conditions during periods of germination. Growth
432 conditions for established plants however seemed more suitable in the upper salt marsh (i.e.
433 larger size of individuals). These observations highlight the relatively small-scale differences
434 in population dynamics of *Salicornia* spp.. The relative importance of seed deposition versus
435 seedling emergence and mortality requires further investigation for all *Salicornia* species and
436 subspecies to fully explain the effects of the environmental gradient.

437 Overall the monitoring data suggests that the experimental islands are not only more
438 isolated from the source population but also more exposed to wave attack and temperature
439 minima during winter. This has to be considered for future analyses of the community
440 development and will be met with frequent monitoring of abiotic parameters. The sediment
441 within the bare islands was eroded by wave scouring down to the artificial groundwater level
442 of all six bare islands during a major storm event with 2 m wave height around the islands
443 (Elon/Felix winter storm in January 2015). We addressed this by installing polycarbonate
444 covers directly on top of each 1 x 1 m cage during the following stormy season between October

445 and March (Fig. S7). The perforated covers allow gas, water and seed exchange and
446 successfully reduced scouring during the storm season of 2015/16. Although physical
447 disturbance is part of the dynamics of salt marsh habitats, we acknowledge that this severe
448 erosion may have led to limited colonisation success of the bare islands in the first year as
449 potentially deposited seeds during the autumn may have been eroded during the January storm.
450 The experiment demonstrated however that unassisted dispersal to the islands was generally
451 possible after one season with a clear selection for early successional species such as *Salicornia*
452 spp. and *S. maritima*. Species-specific differences of early colonisation success is an important
453 criterion for the patch dynamics paradigm in metacommunity ecology (Kneitel and Chase,
454 2004; Winegardner et al., 2012).

455

456 **Conclusion**

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

476

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489

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